UNIVERSITÉ DES ANTILLES ET DE LA GUYANE

DEMANDE D'AUTORISATION D'INSCRIPTION À L'HABILITATION À DIRIGER DES RECHERCHES

NOM : DUYCK

PRÉNOM : Pierre-François

GRADE : Docteur

FONCTION : Chercheur

UNITÉ DE RECHERCHE OU LABORATOIRE D'ACCUEIL : CIRAD – Unité Propre de Recherche 26 – Systèmes de culture bananiers, plantain et ananas

Des traits de vie des bioagresseurs à leurs interactions avec l'agroécosystème

Directeur de recherche ou Parrain s'il y a lieu : Claude BOUCHON, HDR (Université des Antilles et de la Guyane, directeur de l'équipe DYNECAR)

Date de la demande : 5 février 2010

SOMMAIRE

UNIVERSITÉ DES ANTILLES ET DE LA GUYANE

DIVISION DE LA SCOLARITÉ

AUTORISATION D'INSCRIPTION
Pour l'obtention de l'habilitation à diriger des recherches
(Arrêté du 23 novembre 1988)
(à remplir en deux exemplaires)

I.N.E. *(Identifiant National Etudiant):* 0993102256Z..... .....
NOM (patronymique) : DUYCK.....PRÉNOM : Pierre-François.....
NOM MARITAL .....SEXE : M ~~ou F~~ (1)

NÉ (E) le 28/11/1977.....A Grande-Synthe (59)..... *(ville, code département)*

NATIONALITÉ : Française ....PROFESSION : Chercheur au CIRAD.....

ADRESSE. CIRAD – PRAM, Quartier Petit-Morne - BP 214, 97285 Le Lamentin Cedex 2 - Martinique.....
TITULAIRE du diplôme de (docteur ou ingénieur)2 : Doctorat en Biologie Animale .....
.....

DELIVRÉ PAR : (3) ...Université de La Réunion.....LE (date) : 9 décembre 2005.....

SOLLICITE L'AUTORISATION DE S'INSCRIRE A LA PRÉSENTATION DU DIPLOME D'HABILITATION A DIRIGER DES RECHERCHES (4) *:*

DISCIPLINE : Ecologie..... SECTION C.N.U. : 67:Biologie des populations et écologie

Dénomination(s) et adresse(s) de(s) l'établissement(s) où le candidat aurait déjà été inscrit en vue de l'obtention de ce diplôme :
.....
.....
.....
.....
Je certifie ne m'être inscrit auprès d'aucun établissement au cours de la présente année universitaire en vue de l'obtention de ce diplôme.

Fait à .Lamentin...., le 27 janvier 2010.....
signature du (de la) candidat (e)

1 Barrer la mention inutile
2 Joindre une photocopie du diplôme ou, pour les diplômes étrangers, une photocopie de la traduction en français
3 Établissement ayant délivré le diplôme de doctorat ou d'ingénieur
4 Documents à joindre :
- un curriculum Vitae
- soit un ou plusieurs ouvrages publiés ou dactylographiés, soit un dossier de travaux. Ils doivent être accompagnés d'une synthèse de l'activité scientifique du candidat faisant apparaître son expérience dans l'animation d'une recherche.

AVIS MOTIVÉ DU ~~DIRECTEUR DE RECHERCHE~~ (si le candidat en a un) OU DU PARRAIN[5]

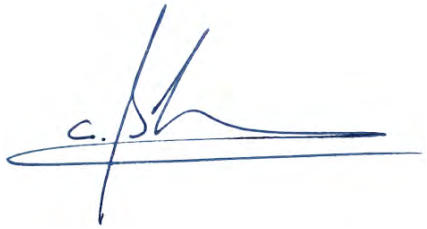
Après avoir étudié le dossier scientifique présenté par M. Pierre-François DUYCK pour une demande d'autorisation de soutenance d'une HDR, j'atteste de la haute qualité des travaux de recherche déjà réalisés par M. DUYCK, ainsi que de celle de ses projets. Par ailleurs, l'examen du dossier montre que les travaux et activités de recherche de M. Duyck sont en adéquation avec le niveau requis par le conseil scientifique de l'UAG pour la section 67 du CNU. Par conséquent, j'émets un avis très favorable pour l'inscription de M. DUYCK à la soutenance d'une HDR.

DISPOSITIONS A PRENDRE, S'IL Y A LIEU, POUR PROTEGER LE CARACTERE CONFIDENTIEL DES TRAVAUX :……
……

NOM, PRÉNOM, QUALITÉ DU DIRECTEUR DE THESE :
QUILICI, Serge, Chercheur CIRAD, HDR……

Fait à Point-à-Pitre, le 1er février 2009

Le parrain : Claude Bouchon



AVIS MOTIVÉ DU CONSEIL SCIENTIFIQUE RESTREINT
……
……
SÉANCE DU……

Fait à ……, le ……

Le Vice-Président du Conseil Scientifique

Le Président de l'Université

AUTORISE

N'AUTORISE PAS [6]

la présente inscription en vue de l'obtention de l'habilitation à diriger des recherches

Fait à Pointe-à-Pitre, le

5 Les candidats extérieurs à l'UAG doivent être parrainés par un enseignant-chercheur de l'établissement titulaire au moins de l'habilitation à diriger des recherches.
6 Barrer la mention inutile

FICHE D'AUTO EVALUATION POUR AUTORISATION INSCRIPTION HDR	
Section CNU : 67:Biologie des populations et écologie	Nom du rapporteur : ……

Nom Prénoms du candidat : **DUYCK Pierre-François**		Situation administrative : Chercheur CIRAD
Nationalité : Française	Année et lieu de naissance : 1977, Grande-Synthe (59)	Âge : 33 ans

FORMATION 3e CYCLE		
DEA ou équivalent : titre, mention DESS Technologies du Végétal	Université : Faculté des Sciences d'Angers	Année d'obtention du DEA : 2000
Doctorat : Compétition interspécifique et capacités invasives. Le cas des Tephritidae de l'île de La Réunion		
Directeur (s) de thèse : Serge QUILICI		
Doctorat : Mention très honorable avec félicitations du jury	Université : Université de La Réunion	Année d'obtention du doctorat : 2005
Post-doc : « Déterminants biodémographiques de la durée de vie chez les insectes » sous la direction de James R. CAREY (Université de Californie, Davis)		

ACTIVITÉS SCIENTIFIQUES			
Unité de recherche à laquelle appartient le(la) candidat(e) : CIRAD, Unité Propre de Recherche 26 – Système de culture bananier, plantain et ananas			
Nom et qualité du directeur de recherche ou du tuteur : Claude BOUCHON, HDR (Université des Antilles et de la Guyane, directeur de l'équipe DYNECAR)			
Date de publication la plus ancienne : 2002 Date de publication la plus récente : 2010			
Citer au maximum 5 revues principales dans lesquelles le candidat a publié : ● Ecology ● Journal of Animal Ecology ● Diversity and Distributions ● Soil Biology and Biochemistry ● Biological Invasions			
Publications avant thèse	● dans revue à comité de lecture	Nombre : 6	Total : 7
	● autre revue	Nombre : 1	
Publications après thèse	● dans revue à comité de lecture	Nombre : 11	Total : 12
	● autre revue	Nombre : 1	
Ouvrages :		Nombre :	
Communications/posters	● dans des congrès internationaux	Nombre : 17	Total : 19
	● dans des congrès nationaux	Nombre : 2	
Rapports divers (contrats et travaux scientifiques)		Nombre :	
Brevets :	Date de la demande :		

ACTIVITÉS D'ENCADREMENT

Activités d'encadrement après la thèse (recherche) :

Doctorants :

2009-2012 : Montage et encadrant principal de la thèse de Grégory Mollot, ED SIBAGHE, Etude des régulations biologiques de *Cosmopolites sordidus* dans les réseaux trophiques des bananeraies, approches isotopiques et modélisation, Directrice : Françoise Lescourret (INRA-PSH, Avignon).

2007-2010 : Participation à l'encadrement de la thèse de **Fabrice Vinatier** sur les aspects Ecologie/Entomologie, ED SIBAGHE, Modélisation spatialisée de l'épidémiologie du charançon du bananier en interaction avec le système de culture et l'organisation paysagère, Directrice : Françoise Lescourret (INRA-PSH, Avignon).

→ 3 articles avec le doctorant en premier auteur (1 publié, 2 soumis)
→ 1 article soumis avec le doctorant en co-auteur

Master 2 :

2009 : Rémy Kulagowski Stage M2. ENITA Bordeaux, « Influence d'une gamme d'intensification de systèmes de culture sur le réseau trophique du charançon du bananier *Cosmopolites sordidus* (Germar). »

2008 : Anaïs Lavigne. Stage M2. Agrocampus Ouest. « Etude de la structure des réseaux trophiques des bananeraies antillaises par approche isotopique. Potentialités de régulation des bioagresseurs. »
→ 1 article soumis avec l'étudiante en co-auteur

Membre de comités de thèse :
- Fabrice Vinatier, CIRAD UR26, PRAM, Martinique. (2007-2010) Modélisation spatialisée de l'épidémiologie du charançon du bananier en interaction avec le système de culture et l'organisation paysagère.
- Cathy Jacquard, UMR PVBMT, La Réunion (2009-2011). Structuration génétique des populations et compétition interspécifique au sein du complexe des Dacini nuisibles aux Cucurbitaceae à l'Ile de La Réunion.
- Pasquale Ciliberti, University of Amsterdam, Pays-Bas (2010-2012) Potential invasion of Afro-tropical an Indo-Australian Tephritidae in Europe

Autres activités et responsabilités:

Evaluation de manuscrits pour revues internationales:
Ecology, *Global Change Biology*, *Diversity and Distributions*, *Biological Invasion*, *Biological Journal of the Linnean Society*, *Animal Behaviour*, *Crop protection, Journal of Economic Entomology*, *Environmental Entomology*, *Entomologia Experimentalis et Applicata*, *Journal of Applied Entomology*, *Crop Protection*, *Fruits*, *African Entomology*, *African Journal of Agricultural Research*

Evaluation de bourses de recherche:
International Foundation for Science (IFS), soutenant les projets de jeunes chercheurs dans les pays en voie de développement

Date : 5 /2/ 2010

Signature du candidat

R É P U B L I Q U E F R A N Ç A I S E

MINISTERE DE LA JEUNESSE DE L'EDUCATION NATIONALE ET DE LA RECHERCHE

UNIVERSITÉ DE LA RÉUNION

DOCTORAT

GRADE DE DOCTEUR

Vu le code de l'éducation, et notamment son article L.613-1

Vu l'arrêté du 25 avril 2002 relatif aux études doctorales

Vu le procès-verbal du jury attestant que l'intéressé a soutenu, le 9 décembre 2005 une thèse portant sur le sujet suivant : Compétition interspéficique et capacités invasives. Le cas des Tephritidae de l'Ile de La Réunion devant un jury présidé par BERNARD REYNAUD, DIRECTEUR DE RECHERCHE HDR et composé de PATRICE DAVID, CHARGE DE RECHERCHE HDR, JEAN PAUL MONGE, PROFESSEUR DES UNIVERSITES, SERGE QUILICI, DIRECTEUR DE RECHERCHE HDR, CHRISTOPHE THEBAUD, PROFESSEUR DES UNIVERSITES

Vu la décision dudit jury prononçant l'admission de l'intéressé *avec la mention très honorable avec félicitations*

le Diplôme de docteur de Biologie Animale de l'Université de La REUNION est délivré à **M. PIERRE-FRANCOIS DUYCK** né le 28 novembre 1977 à GRANDE SYNTHE (059) pour en jouir avec les droits et prérogatives qui y sont attachés et confère le grade de docteur.

Fait à Saint Denis, le 18 avril 2006

Le titulaire

Le Président

Pour le Président
Le Vice-Président
du Conseil des Etudes et
de la Vie Universitaire

Jean-Claude GATINA

UNIVERSITÉ DE LA RÉUNION

Le Recteur d'Académie,
Chancelier des universités

Paul CANIONI

RECTORAT ST DENIS-REUNION

N° REUNIO 5632763
/2006200500008

CURRICULUM VITAE

Nationalité :	Française
Date de naissance :	Né le 28 Novembre 1977 à Grande-Synthe (59)
Adresse professionnelle :	CIRAD-PRAM BP 214 – 97285 Le Lamentin Cedex 2 Téléphone : 05 96 42 30 47 Fax : 05 96 42 30 01 Adresse électronique : duyck@cirad.fr
Profession :	**Chercheur, Docteur en biologie animale**
Fonction actuelle :	**Chercheur en écologie dans l'Unité Propre de Recherche 26 – Système de culture bananier, plantain et ananas, affecté au Pôle de Recherche Agro-environnementale de Martinique (PRAM)**
Organisme :	Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) Département PERSYST
Diplômes, titres universitaires :	**- Thèse de Doctorat en Biologie Animale (UMR PVBMT - Université de La Réunion)** - Mention très honorable avec félicitations du jury – soutenue le 9 décembre 2005, Directeur : Serge QUILICI Jury : Christophe THEBAUD, Patrice DAVID, Jean-Paul MONGE, Serge QUILICI, Bernard REYNAUD - DESS « Technologie du végétal » - (Faculté des Sciences d'Angers / I.N.H.), Mention Bien (2000) 1995 - 1999 : Faculté Libre des Sciences (Lille) : - Maîtrise de Biologie des Populations et des Ecosystèmes, Mention Assez-Bien - Licence de Biologie des Organismes, Mention Assez-Bien - DEUG Science de la Vie, Mention Assez-Bien
Langues	**Langue maternelle :** Français **Langue de travail :** Anglais
Expérience professionnelle :	**2008 – … :** Chercheur au CIRAD sur l'étude de l'écologie des ravageurs du bananier (charançons et nématodes) au PRAM, Martinique (UPR 26) **2007 :** Contrat postdoctoral « Déterminants biodémographiques de la durée de vie chez les insectes ». Financement postdoctoral à l'université de Californie (Davis) avec James R. CAREY / Accueil à l'UMR PVBMT, CIRAD Réunion **2006 :** Chercheur associé à l'UMR PVBMT (Pôle de Protection des Plantes (3P), Université de La Réunion) - démographie comparée et coexistence entre un biotype invasif et un biotype indigène chez *Bemisia tabaci* (en collaboration avec H. DELATTE et B. REYNAUD, CIRAD Réunion). - analyses des traits de vie chez différentes espèces de Tephritidae (en collaboration avec T. BREVAULT, CIRAD Cameroun ; J.F. VAYSSIERES, CIRAD Bénin).

	2003 – 2005 : Thèse de Doctorat (Mention très honorable avec félicitations du jury) à l'UMR PVBMT, 3P, CIRAD Réunion avec plusieurs séjours de plusieurs mois au CEFE/CNRS, «Compétition interspécifique et capacités invasives. Le cas des Tephritidae de l'île de La Réunion» **2002 :** CDD Cadre CIRAD (3P, CIRAD Réunion) - Surveillance et étude de la biologie et du comportement de la mouche de la pêche. **2001 - 2002 :** Volontaire à l'aide technique au CIRAD Réunion: - Optimisation d'attractifs alimentaires pour la mouche du melon - Suivi de la dynamique des populations de la teigne du chou et d'aleurodes et de leurs parasitoïdes respectifs. **2000** – Stage de DESS au laboratoire d'entomologie du CIRAD-FLHOR, La Réunion.
Distinctions scientifiques et honorifiques	Nominé lors du concours « Jeunes Chercheurs 2004» de l'Institut Français de la Biodiversité (IFB).
Evaluation de manuscrits pour revues internationales :	*Ecology, Global Change Biology, Diversity and Distributions, Biological Invasion, Biological Journal of the Linnean Society, Animal Behaviour, Crop protection, Journal of Economic Entomology, Environmental Entomology, Entomologia Experimentalis et Applicata, Journal of Applied Entomology, Crop Protection, Fruits, African Entomology, African Journal of Agricultural Research*
Evaluation de projets :	Bourses de recherche de l'*International Foundation for Science* (IFS), soutenant les projets de jeunes chercheurs dans les pays en voie de développement
Compétences	**Techniques de laboratoire et de terrain :** Elevage de différentes espèces d'insectes ; Mise au point d'expérimentations sur le développement et le comportement des insectes ; Collectes sur le terrain (pour connaissance de la distribution géographique, efficacités de systèmes de piégeages) **Analyses (réalisées avec le logiciel R) :** Calcul et statistiques des différents paramètres démographiques ; Modélisation de la distribution d'espèces en fonction de variables environnementales ; Modèles Linéaires Généralisés ; Analyses de Variance et Co-variance ; Analyses Multivariées.

LISTE DES PUBLICATIONS

Tableau récapitulatif des publications par année et par revue, classées par ordre d'Impact Factor 2008 (Articles publiés au 1er janvier 2010)

Revue	IF 2008	Année 2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Ecology	4.9					1					1
Journal of Animal Ecology	4.2					1					1
Diversity and Distributions	3.4						1				1
Soil Biology and Biochemistry	2.9								1		1
Biological Invasions	2.8								1		1
Ecological Modelling	2.2								1		1
Applied Soil Ecology	2.2									1	1
Ecological Entomology	1.9			1				2			3
Bulletin of Entomological Research	1.4	1		1							2
Entomologia Experimentalis et Applicata	1.3								1		1
Journal of Economic Entomology	1.3		1	1							2
Environmental Entomology	1.2							1			1
Annals of the Entomological Society of America	1.2				1						1
Total		1	1	3	1	2	1	3	4	1	**17**

Articles publiés dans revue à comité de lecture à facteur d'impact:
(* = articles donnés en annexe de ce document)

[P17] Chabrier C., Tixier P., Duyck P.F., Carles C, & Quénéhervé P. (**2010**) Factors influencing the survivorship of the burrowing nematode, *Radopholus similis* (Cobb.) Thorne in two types of soil from banana plantations in Martinique. ***Applied Soil Ecology***, 44, 116-123

*[P16] Duyck, P.F., Pavoine, S., Tixier, P., Chabrier, C. & Quénéhervé, P. (**2009**) Host range as an axis of niche partitioning in the plant-feeding nematode community of banana agroecosystems. ***Soil Biology & Biochemistry***, 41, 1139-1145.

*[P15] Vinatier, F., Tixier, P., Le Page, C., Duyck, P.F., & Lescourret, F. (**2009**) COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. ***Ecological Modelling***, 220, 2244-2254.

[P14] Delatte, H., Duyck, P.F., Triboire, A., David, P., Becker, N., Bonato, O. & Reynaud, B. (**2009**) Differential invasion success among biotypes. Case of *Bemisia tabaci*. ***Biological Invasions***, 11, 1059-1070.

[P13] Kouloussis, N.A., Papadopoulos, N.T., Müller, H-G., Wang, J-L., Mao, M., Katsoyannos, B.I., Duyck, P.F., & Carey, J.R. (**2009**) Life table assay of field-caught Mediterranean fruit flies, Ceratitis capitata, (Diptera: Tephritidae) reveals age bias. ***Entomologia Experimentalis et Applicata***, 132, 172-181.

[P12] Duyck, P.F., David, P., Pavoine, S. & Quilici, S. (**2008**) Can host-range allow niche differentiation of invasive polyphagous fruit flies (Diptera: Tephritidae) in La Réunion? ***Ecological Entomology***, 33, 439-452.

[P11] Brévault, T., Duyck, P.F., & Quilici, S. (**2008**) Life-history strategy in an oligophagous tephritid: the tomato fruit fly, *Neoceratitis cyanescens*. ***Ecological Entomology***, 33, 529-536.

[P10] Vayssières, J.F., Carel, Y., Coubes, M. & Duyck, P.F. (**2008**) Development of immature stages and comparative demography of two cucurbit-attacking fruit flies in Reunion island: *Bactrocera cucurbitae* and *Dacus ciliatus* (Diptera Tephritidae). ***Environmental Entomology***, 37, 307-314.

*[P9] Duyck, P.F., David, P., & Quilici, S. (**2007**) Can more *K*-selected species be better invaders? A case study of fruit flies in La Réunion. ***Diversity and Distributions***, 13, 535-543.

*[P8] Duyck, P.F., David, P., Junod, G., Brunel, C., Dupont R. & Quilici, S. (**2006**) Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion Island. ***Ecology***, 87, 1170-1780.

[P7] Duyck, P.F., David, P., & Quilici, S. (**2006**) Climatic niche partitioning following successive invasions by fruit flies in La Réunion. ***Journal of Animal Ecology***, 75, 518-526.

[P6] Rousse, P., Duyck, P.F., Quilici, S., & Ryckewaert, P. (**2005**) Adjustment of field cage methodology for testing food attractants for fruit flies (Diptera: Tephritidae). ***Annals of the Entomological Society of America***, 98, 402-408.

[P5] Duyck, P.F., David, P., & Quilici, S. (**2004**) A review of relationships between interspecific competition and invasions in fruit flies (Diptera : Tephritidae). ***Ecological Entomology***, 29, 511-520.

[P4] Duyck, P.F., Rousse, P., Ryckewaert, P., Fabre, F., & Quilici, S. (**2004**) Influence of adding borax and modifying pH on effectiveness of food attractants for melon fly (Diptera: Tephritidae). ***Journal of Economic Entomology***, 97, 1137-1141.

[P3] Duyck, P.F., Sterlin, J.F., & Quilici, S. (**2004**) Survival and development of different life stages of *Bactrocera zonata* (Diptera: Tephritidae) reared at five constant temperatures compared to other fruit fly species**. *Bulletin of Entomological Research***, 94, 89-93.

[P2] Fabre, F., Ryckewaert, P., Duyck, P.F., Chiroleu, F., & Quilici, S. (**2003**) Comparison of the efficacy of different food attractants and their concentration for melon fly (Diptera: Tephritidae). ***Journal of Economic Entomology***, 96, 231-238.

[P1] Duyck, P.F. & Quilici, S. (**2002**) Survival and development of different life stages of three *Ceratitis* spp. (Diptera: Tephritidae) reared at five constant temperatures. ***Bulletin of Entomological Research,*** 92, 461-469.

Articles soumis dans revue à comité de lecture à facteur d'impact:

[S1] Duyck, P.F., Lavigne, A., Vinatier, F., Achard, R., & Tixier, P. Cover crop alters trophic position of generalist predators in litter of banana agroecosystem. (***Oecologia***)

[S2] Tixier, P., Côte, F.X., Duyck, P.F., Caron-Lormier, G. & Malézieux, E. Computational agro-ecology: toward food web-based simulation. (***BioScience***)

[S3] Vinatier, F., Chailleux, A., Duyck, P.F., Lescourret, F. & Tixier, P. Radio telemetry unravels movements of a walking insect species in heterogeneous environments (***Animal Behaviour***)

[S4] Vinatier, F., Tixier, P., Duyck, P.F., & Lescourret, F. Factors and mechanisms explaining spatial heterogeneity. A review of methods for insect populations (***Methods in Ecology and Evolution***).

[S5] Chabrier, C., Tixier, P, Duyck, P.F. & Quénéhervé, P. Survival of the burrowing nematode *Radopholus similis* (Cobb) Thorne without food: why do males survive so long? (***Applied Soil Ecology***)

Chapitre d'ouvrage:

Quilici S. & Duyck P.F. (**2010**) Mouches des fruits invasives : L'exemple du genre *Bactrocera*. Maladies émergentes chez les plantes, les animaux et l'homme : Stratégies et méthodes d'analyse épidémiologique (ed. by I. Sache and J. Barnouin). Editions QUAE, à paraître.

Autres articles publiés:

Duyck, P.F., & Quilici, S. (**2007**) Interspecific competition and invasion ability in Tephritidae: A case study in Reunion island. ***TEAM Newsletter***, No 5 - December 2007, 2-5.

Quilici, S., Duyck, P.F., Rousse, P., Gourdon, F., Simiand, C. & Franck, A. (**2005**) La mouche de la pêche sur mangue, goyave, etc. A La Réunion, évolution des recherches et des méthodes de lutte. ***Phytoma – La Défense des Végétaux***, 584, 44-47.

Communications lors de congrès (communications orales, communications invitées et proceedings):

2009 Conference ISEM. Ecological modelling for enhanced sustainability in management, October 6-9, 2009, Québec, Canada

- Linking cropping system and food web models to assess agroecosystem community stability: Example of litter macrofauna in banana systems. Tixier, P & Duyck, P.F. (communication orale)

Farming Systems Design, International symposium on Methodologies for Integrated Analysis of Farm Production Systems, , August 23-26 2009, Monterey, USA

- COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. Vinatier, F., Tixier, P., Le Page, C., Duyck, P.F., & Lescourret, F. (communication orale)

2008 1st Meeting of TEAM (Tephritid Workers of Europe Africa and the Middle East), 7-8 April 2008, Palma de Mallorca, Spain.

- The demography of invasion: Tephritids of La Reunion, a unique model to study invasion and competition. Duyck, P.F., & Quilici S. (communication orale invitée)

VIIème Conférence OILB sur la Production Fruitière Intégrée, 27-30 octobre 2008, Avignon, France.

- COSMOS, a spatially explicit model to simulate the epidemiology of banana weewil (*Cosmopolites sordidus*). Vinatier, F., Tixier, P., Le Page, C., Bruchou, C., Duyck, P.F., & Lescourret, F. (poster)

2007 Proceedings of a final research coordination meeting organized by the joint FAO/IAEA programme, Vienna, Austria.

- Development of improved attractants and their integration into fruit fly SIT management programmes : final report for the period 2001-2005

Quilici, S., Franck, A., Duyck, P.F., Rousse, P., Ryckewaert, P., Simiand, C. (communication + proceedings)

2006 VII International Symposium on Fruit Flies of Economic Importance, Salvador de Bahia, Brazil.
- Interspecific competition and related demographic traits explain successive invasions by fruit flies in La Réunion. Duyck, P.F., David, P., Junod, G., Brunel, C., Dupont, R. & Quilici. S. (communication orale + poster)
- Niche partitioning via climate and host-plants following successive invasions by fruit flies in La Réunion. Duyck, P.F., David, P. & Quilici S. (poster)

2nd RCM of the FAO-IAEA on improving sterile male performance in fruit fly SIT, Salvador de Bahia, Brazil. Influence of exposure to methyleugenol on mating success of males in the Peach fruit fly, Bactrocera zonata. Duyck, P.F., Franck, A. & Quilici S. (communication orale)

2005 IX International Congress of Ecology; 90th Annual Meeting of the Ecological Society of America, Montréal, Canada. Interspecific competition and invasive ability. A case study of Tephritidae in La Réunion Island. Duyck, P.F., David, P. & Quilici S. (communication orale)

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- Life history traits as predictors for biological invaders? Duyck, P.F., David, P., Glénac, S. & Quilici S. (communication orale)
- Humidity and host-plant as important factors influencing the pre-imaginal development of fruit flies (Diptera: Tephritidae). Duyck, P.F., David, P., Glénac, S. & Quilici S. (poster)

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Final research co-ordination meeting on quality assurance of mass produced and released fruit flies, Chiapas, Mexique. Relationships between host-fruit, pupal weight and fecundity in fruit flies (Diptera: Tephritidae). Duyck, P.F., David, P, Brunel, C. & Quilici S. (communication orale)

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2002 VI International Symposium on Fruit Flies of Economic Importance, Stellenbosch, Afrique du Sud.

- Comparative study of the developmental biology of three species of fruit flies (*Ceratitis* spp.) (Diptera: Tephritidae), pests of fruit crops in Reunion Island. Duyck, P.F., Quilici S. & Glénac S. (poster + proceedings)
- Comparison and optimisation of the efficacy of different food attractants for both sexes of the melon fly (Diptera: Tephritidae). Duyck, P.F., Quilici, S., Fabre, F. & Ryckewaert, P. (poster + proceedings)

2001 Annual Meeting of Agricultural Scientists, Le Réduit, Mauritius. Etude comparée de la biologie du développement chez trois espèces de mouches des fruits (*Ceratitis* spp.) (Diptera: Tephritidae), nuisibles aux cultures fruitières à La Réunion. Duyck, P.F., Quilici S. (communication orale + proceedings)

ACTIVITES D'ENCADREMENT

Encadrement de Doctorants

2009 - 2012 : Montage et encadrant principal de la thèse de Grégory Mollot, ED SIBAGHE, Etude des régulations biologiques de *Cosmopolites sordidus* dans les réseaux trophiques des bananeraies, approches isotopiques et modélisation, Directrice : Françoise Lescourret (INRA-PSH, Avignon).

2007 – 2010 : Participation à l'encadrement de la thèse de **Fabrice Vinatier** sur les aspects Ecologie/Entomologie, ED SIBAGHE, Modélisation spatialisée de l'épidémiologie du charançon du bananier en interaction avec le système de culture et l'organisation paysagère, Directrice : Françoise Lescourret (INRA-PSH, Avignon).

→ **3 articles avec le doctorant en premier auteur (1 publié : P15, 2 soumis : S3, S4)**

→ **1 article soumis avec le doctorant en co-auteur (S1)**

Membre de comités de thèse :

- Fabrice Vinatier, CIRAD UR26, PRAM, Martinique. (2007-2010) Modélisation spatialisée de l'épidémiologie du charançon du bananier en interaction avec le système de culture et l'organisation paysagère.
- Cathy Jacquard, UMR PVBMT, La Réunion (2009-2011). Structuration génétique des populations et compétition interspécifique au sein du complexe des Dacini nuisibles aux Cucurbitaceae à l'Ile de La Réunion.
- Pasquale Ciliberti, University of Amsterdam, Pays-Bas (2010-2012) Potential invasion of Afro-tropical an Indo-Australian Tephritidae in Europe

Encadrement de stagiaires de Master 2

2009 : Rémy Kulagowski Stage M2. ENITA Bordeaux, « Influence d'une gamme d'intensification de systèmes de culture sur le réseau trophique du charançon du bananier *Cosmopolites sordidus* (Germar). »

2008 : Anaïs Lavigne. Stage M2. Agrocampus Ouest. « Etude de la structure des réseaux trophiques des bananeraies antillaises par approche isotopique. Potentialités de régulation des bioagresseurs. »

→ **1 article soumis avec l'étudiante en co-auteur (S1)**

2004 : Caroline Brunel. Stage M2. INH Angers, « Aspects de la compétition chez les Diptères Tephritidae : Mise en évidence de phéromones de marquage, relations entre poids des pupes et potentiel biotique »

→ **1 article publié avec l'étudiante en co-auteur (P8)**

2004 : Guillemette Junod . Stage M2. ENSAIA Nancy, " La compétition larvaire interspécifique chez les Tephritidae : cas de quatre espèces de mouches des fruits de l'île de la Réunion ».

→ **1 article publié avec l'étudiante en co-auteur (P8)**

2004 : Raphaël Dupont. Stage M2 INH Angers, «Stimuli olfactifs et compétitivité dans l'appropriation du fruit-hôte par quatre espèces de Tephritidae de l'île de la Réunion ».

→ **1 article publié avec l'étudiant en co-auteur (P8)**

2002 : Joseph Sterlin. Stage M2. AgroParisTech, Paris, « Etude de la biologie et du comportement de *Bactrocera zonata* (Saunders), mouche des fruits invasive à l'île de La Réunion »

→ **1 article publié avec l'étudiant en co-auteur (P3)**

DES TRAITS DE VIE DES BIOAGRESSEURS A LEURS INTERACTIONS AVEC L'AGROECOSYSTEME

Pourquoi s'inscrire dans une démarche d'HDR à l'UAG ?

Un objectif de mon inscription en HDR est de permettre de réaliser un bilan sur mon expérience et la cohérence de mes recherches, afin de proposer des projets novateurs et de qualité aux étudiants sous mon encadrement. J'ai encadré plusieurs étudiants de Master 2, et je suis actuellement encadrant principal d'un étudiant en doctorat (Grégory Mollot) et participe à l'encadrement d'un deuxième doctorant (Fabrice Vinatier). L'HDR est l'occasion d'une réflexion approfondie sur les résultats d'un chercheur et de débattre des projets de recherche à soumettre aux étudiants.

L'UR 26 du CIRAD étant principalement basée dans les Antilles, constituée d'environ 10 chercheurs répartis entre Martinique (Pôle de Recherche Agro-environnementale de la Martinique, PRAM) et Guadeloupe, mon unité de recherche pourrait participer à la formation des étudiants, en particulier en accueillant en doctorat des étudiants formés à l'UAG.

Enfin dans une perspective de futures collaborations, cette démarche est l'occasion d'échanges privilégiés avec les chercheurs des unités de recherche de l'UAG. L'écologie, en particulier l'écologie des communautés et la thématique des réseaux trophiques étant au centre de mes projets de recherche, il sera possible d'interagir avec des unités de l'UAG ayant des axes de recherche proches comme DYNECAR en Guadeloupe et ECOFOG en Guyane.

Introduction

Au cours de mon expérience de chercheur, je me suis intéressé à différents aspects de l'écologie des bioagresseurs allant de l'étude de leurs traits de vie jusqu'à leurs interactions avec l'agroécosystème. Je me suis intéressé à différents modèles biologiques : les mouches des fruits de la famille des Tephritidae, (4 espèces infestant les cultures fruitières et 3 espèces infestant les cultures maraichères), 2 biotypes de l'aleurode *Bemisia tabaci* (Hemiptera: Aleyrodidae), les nématodes phytophages dans les bananeraies (6 espèces appartenant à différentes familles), le charançon du bananier *Cosmopolites sordidus* (Coleoptera: Curculionidae) et différentes espèces (prédateurs et phytophages) appartenant au réseau trophique de ce dernier. Ma démarche scientifique va dans le sens d'une prise en compte d'une complexité croissante des interactions avec les espèces. Cette évolution s'est accompagnée également de l'utilisation de méthodes d'étude, en particulier en biostatistiques et en modélisation, de plus en plus complexes et diverses.

J'ai orienté mes recherches suivant deux axes : (i) la biodémographie et le comportement des bioagresseurs et (ii) les interactions entre espèces et avec les facteurs environnementaux. L'étude des traits de vie des espèces est essentielle car ceux-ci vont conditionner les interactions entre les espèces et l'environnement et *in fine* leur épidémiologie et leurs dégâts sur les cultures. L'étude des systèmes de piégeages et la connaissance de leurs biais est importante pour la mise au point de moyens de lutte contre les bioagresseurs des cultures mais également nécessaire pour les études sur la dynamique et la distribution spatiale des populations. Aussi, les comportements des bioagresseurs, en particulier ceux liés à la mobilité vont influencer les capacités de dispersion et donc la dynamique spatiale.

Les différents traits de vie des bioagresseurs vont conditionner les interactions entre les espèces comme la compétition interspécifique ou la prédation, ainsi que les interactions avec les facteurs biotiques et abiotiques du milieu. Ces facteurs permettent notamment de caractériser les niches écologiques des espèces et conditionnent leurs possibilités de coexistence, notamment pour les espèces de bioagresseurs envahissantes introduites dans une communauté déjà établie. Les traits de vie comme la fécondité, la mortalité et les capacités de dispersion contribuent également à comprendre et à modéliser la dynamique temporelle et spatiale des populations de bioagresseurs sur le terrain.

En perspective, deux nouveaux projets de recherche sont proposés dans la continuité de cette synthèse. Le premier projet de recherche porte sur la caractérisation de l'habitat des bioagresseurs, la dynamique et la dispersion des populations en milieux hétérogènes. Le deuxième projet de recherche s'intéresse à la caractérisation et la modification du réseau trophique du charançon du bananier par les pratiques culturales. Il s'agit notamment d'identifier les liens trophiques entre espèces et la façon dont ils peuvent être modifiés dans l'objectif d'augmenter la régulation potentielle du bioagresseur.

I. Document de synthèse de l'activité scientifique

I.A) Biodémographie et comportement des bioagresseurs

I.A.1) Traits de vie et influence des facteurs de l'environnement

Publications : P1, P3, P7, P10, P11, P12, P14, P17, S5 ; P=article publié ; S=article soumis

L'étude des traits de vie des bioagresseurs est essentielle pour une meilleure connaissance de l'interaction des espèces avec le milieu environnant. Les traits de vie, comme la longévité, la fécondité et la taille, ont un lien direct avec la niche trophique, l'aptitude à la compétition et les tolérances aux facteurs biotiques et abiotiques du milieu. Dans la synthèse présentée ci-après, les résultats de travaux sur la caractérisation des paramètres démographiques et l'influence de facteurs du milieu (température, humidité, plante-hôtes, type de sol et potentiel hydriques) sur les traits de vie de différentes espèces sont présentés.

Les stratégies démographiques des insectes sont liées à leurs fonctions écologiques dans l'écosystème (Schowalter, 2000). Chez les insectes phytophages, ces traits biologiques dépendent principalement de la gamme de plantes-hôtes (Bernays & Chapman, 1994). Nous avons montré que chez les mouches des fruits de la famille des Tephritidae, les paramètres démographiques (basés sur la fécondité et la longévité) dépendent de l'envergure de la gamme de plantes-hôtes des espèces considérées. Une espèce oligophage comme la mouche de la tomate, *Neoceratitis cyanescens*, montre des traits de vie intermédiaires entre les Tephritidae polyphages et monophages [P11]. Ses pontes, de taille plus réduite comparées aux espèces polyphages, et sa spécialisation sur la famille des Solanaceae, dont les fruits contiennent des composés toxiques, participent à réduire la compétition intra- et inter- spécifique.

Les plantes-hôtes ont également un effet direct sur la survie et le temps de développement des larves de Tephritidae. La nature du fruit-hôte peut affecter le développement des mouches des fruits par des effets directs sur la survie pré-imaginale, le temps de développement pré-imaginal et le poids pupal (Fitt, 1986) mais aussi par des effets indirects sur la fécondité *via* le poids pupal (Krainacker *et al.*, 1987; Krainacker *et al.*, 1989). Chez quatre espèces de mouches des fruits de La Réunion, les quatre plantes-hôtes principales (goyave, mangue,

goyavier de Chine, badamier) ont montré une influence marquée sur les différents traits de vie étudiés [P12]. Comme conséquence, le taux de reproduction net R_0 est largement dépendant du fruit-hôte.

La température a une influence très importante sur le développement et la survie des insectes (Dangles *et al.*, 2008). Celle-ci a été étudiée séparément sur les différents stades de développement préimaginaux: embryonnaire, larvaire, pupal, et sur la maturation ovarienne des femelles adultes. Chez différentes espèces de mouches des fruits et d'aleurodes, la survie et le temps de développement ont été mesurés pour une série de températures constantes pour les différents stades. Les seuils minimums de développement des différents stades ont été calculés pour 6 espèces de Tephritidae de La Réunion : 4 espèces infestant les cultures fruitières [P1, P3] et 2 espèces infestant les Cucurbitaceae [P10]. Un travail similaire a également été réalisé afin de comparer 2 biotypes d'aleurodes de l'espèce *Bemisia tabaci* (Hemiptera: Aleyrodidae) [P14]. Ces résultats permettent de prédire l'accroissement des populations grâce aux seuils de développement et aux constantes thermiques (Wagner *et al.*, 1984), d'expliquer la distribution et de prévoir les zones potentielles d'invasion dans le monde.

L'humidité peut également affecter le développement des Tephritidae de plusieurs façons. Tsitsipis & Abatzis (1980) ont montré que la dessiccation affecte fortement l'éclosion des oeufs chez *Bactrocera oleae*. Cependant, dans la nature, les oeufs et les larves des Tephritidae se développent à l'intérieur des fruits qui procurent un milieu protecteur avec une forte teneur en eau. Les adultes ont besoin de peu d'eau pour survivre, et la trouvent dans la nature sous forme d'eau libre, de nectar produit par les plantes, de fruit décomposé ou de miellat (Prokopy & Roitberg, 1984). On suppose généralement que les mouches des fruits adultes satisfont leur faible besoin en eau lors de la recherche de protéines (Meats, 1989). D'un autre côté, les pupes étant le seul stade présent dans le sol, l'humidité du sol a un effet direct et important sur le développement pupal des Tephritidae (Eskafi & Fernandez, 1990). L'influence de l'humidité relative et de l'immersion temporaire sur le développement de quatre Tephritidae de La Réunion a donc été étudiée sur le stade pupal [P7]. Il a été montré que les différentes espèces étudiées avaient des tolérances très différentes à la sécheresse et à l'humidité et que pour la plupart des espèces, il y a un compromis entre ces deux aptitudes.

Concernant les bioagresseurs du sol, la solution, le potentiel hydrique et le type de sol ont une influence majeure sur leur survie (De Waele & Elsen, 2007). La survie des nématodes *Radopholus similis* et *Pratylenchus coffeae*, principaux bioagresseur du bananier au niveau mondial, a été étudiée en fonction de différents sols (Andosol et Nitisol) et sur une gamme de potentiels hydriques [P17]. La survie des nématodes augmente quand les sols sont humides (proches de la capacité au champ). *R. similis* survit plus longtemps dans les Nitisols que dans les Andosols, ce qui n'est pas le cas pour *P. coffeae* dans les sols humides. *P. coffeae* a une longévité plus longue que *R. similis* dans les deux types de sol. D'un point de vue appliqué ces résultats montrent que la durée des jachères sans plantes-hôtes pour assainir les sols ne peut être réduite à moins d'une année sans risques. La survie de *R. similis* a également été étudiée dans différentes solutions aqueuses afin de mieux comprendre le risque de dissémination par les eaux de ruissellement [S5]. Les résultats montrent une survie très faible des femelles comparée à celle des mâles, et suggèrent une allocation des ressources des femelles envers des comportements de recherche et de ponte d'œufs au détriment de la survie, en l'absence des plantes-hôtes.

I.A.2) Comportement et piégeages des insectes

Publications : P2, P4, P6, P13, S3 ; P=article publié ; S=article soumis

Le comportement des bioagresseurs vis-à-vis des systèmes de piégeage est à la fois important d'un point de vue appliqué en tant que moyen de lutte ou de surveillance, mais

également nécessaire pour des études sur la dynamique des populations et la distribution des espèces. Les objectifs ont été de maximiser l'efficacité des systèmes de piégeage et d'estimer les biais engendrés par ceux-ci.

Un premier axe de recherche était lié à la mise au point de traitements par tâches pour la lutte contre les mouches des Cucurbitaceae. Le traitement par tâche consiste au mélange d'un attractif alimentaire et d'un insecticide que l'on pulvérise sur une partie restreinte de la culture au lieu de pulvériser l'ensemble de celle-ci. Pour mettre au point ce type de technique il faut tout d'abord pouvoir comparer et sélectionner des attractifs alimentaires efficaces. Nous avons premièrement mis au point une méthode afin de pouvoir tester un grand nombre de solutions possibles en grandes cages extérieures [P6]. Les pièges doivent notamment être placés aléatoirement au début de l'expérimentation, puis tournés régulièrement pour diminuer l'influence des conditions climatiques. La présence de plantes-hôtes dans la cage permet une meilleure dispersion des mouches et augmente la discrimination potentielle entre traitements. Les femelles initialement privées de protéines et matures donnent de meilleurs pourcentages de recapture. En utilisant cette méthode, l'attractivité de différents hydrolysats de protéines à différentes concentrations a été testée sur la mouche du melon *Bactrocera cucurbitae* [P2]. Il a été montré des différences très importantes entre les produits testés, qui semblent liées au pH des solutions. Nous avons donc étudié ensuite les effets de la modification du pH et de l'ajout de Borax (conservateur généralement ajouté dans les pièges afin de garder les spécimens d'insectes identifiables) sur certains de ces attractifs [P4]. Nous avons montré que le Borax diminue l'efficacité des attractifs et que le pH optimal dépend de l'attractif alimentaire utilisé et de l'espèce considérée.

Lors de mon contrat postdoctoral, je me suis intéressé à la longévité des insectes au champ. Alors que les pièges sont communément utilisés pour échantillonner des insectes pour la recherche ou le contrôle des populations, les biais potentiels provenant de réponses différentes des individus de différents âges n'avaient jamais été examinés. Grâce à la longévité résiduelle d'insectes capturés sur le terrain (Carey *et al.*, 2008), nous avons montré qu'en fonction du type de piégeage utilisé et de la saison de capture, la structure en âge des populations de la mouche méditerranéenne des fruits *Ceratitis capitata* au champ est modifiée [P13].

Le mouvement des individus est un processus fondamental affectant la dynamique des populations des organismes (Chapman *et al.*, 2007), affectant en particulier la recherche d'alimentation, la sélection de l'habitat, et la dispersion (Begon *et al.*, 1996). Dans le cadre de la thèse de Fabrice Vinatier, pour laquelle je participe à l'encadrement sur les aspects entomologie et écologie, nous nous sommes intéressés au comportement de mouvement du charançon du bananier, *C. sordidus* [S3]. Ceci a été réalisé par la mise au point d'une technique de radio-télémétrie (puce RFID, R*adio* F*requency* ID*entification tagging*) permettant d'évaluer le déplacement individuel de chaque charançon. La dispersion est notamment affectée par le pattern de plantation des bananiers et par la présence/absence des résidus de culture.

I.B) Interactions entre espèces et avec les facteurs environnementaux, cas particulier des espèces envahissantes.

L'étude de la répartition et de l'abondance des espèces sur le terrain peut permettre de caractériser les niches écologiques des différentes espèces et donc de faire des hypothèses sur les possibilités de coexistence entre celle-ci. J'ai étudié notamment le cas particulier d'espèces envahissantes en compétition avec les communautés résidentes. En effet en rassemblant des

taxa précédemment isolés, les invasions biologiques ont des effets marqués sur la fonction des écosystèmes et la structure des communautés (Williamson, 1996; Juliano *et al.*, 2002; Lounibos, 2002). Bien que leurs conséquences soient désastreuses (Myers *et al.*, 2000), les invasions biologiques fournissent une opportunité unique d'observer les processus d'assemblage des communautés en temps réel. Prédire comment une communauté va être affectée par les invasions, en se basant sur les traits de vie des espèces envahissantes et des communautés résidentes, est à la fois un enjeu fondamental, ainsi qu'un objectif important pour la conservation et pour la gestion des bioagresseurs.

I.B.1) Relation entre stratégie démographique, aptitude à la compétition et possibilité d'invasion

Publications P5, P8, P9, P14, P=article publié ; S=article soumis

Alors que la prédiction des invasions se basant sur des règles écologiques a eu un certain succès (Hobbs & Huenneke, 1992; Kolar & Lodge, 2001; Levine *et al.*, 2004), l'importance de la compétition interspécifique dans l'aptitude à l'invasion reste ambigüe. Manifestement, la compétition prend place entre les espèces envahissantes et la communauté résidente (Shea & Chesson, 2002). Cependant, ceci ne signifie pas forcément que la compétition agit comme un crible important capable de garder les espèces envahissantes à partir d'un pool d'espèces candidates. Bien que cette hypothèse ou d'autres similaires aient été mises en avant (Byers, 2000; Vila & Weiner, 2004), dans d'autres cas l'accent a été mis sur les traits sélectionnés *r* et sur la capacité des espèces à coloniser des espaces vides (Lodge, 1993; Rejmanek & Richardson, 1996).

Mon premier travail de recherche conduit sur ce sujet a été de dresser un inventaire des cas connus d'invasion chez les Tephritidae polyphages à l'échelle mondiale, en soulignant le rôle probable de la compétition interspécifique dans ces interactions [P5]. J'ai ensuite comparé les traits d'histoire de vie des quatre espèces afin de vérifier si une stratégie démographique particulière était corrélée avec une bonne aptitude à l'invasion [P9]. Enfin, j'ai déterminé l'intensité et l'asymétrie de différents mécanismes de compétition interspécifique (compétition larvaire, interférences entre adultes via les phéromones de marquage, la localisation et la défense de la ressource) afin de savoir s'il existait une hiérarchie de compétition et si elle était en accord avec le rang d'invasion [P8].

Les quatre espèces de Tephritidae étudiées montrent des différences importantes au niveau de leurs traits d'histoire de vie et de leur aptitude à la compétition. Une correspondance entre cette aptitude à la compétition et certains traits des espèces peut être établie. Les données montrent que l'espèce indigène, *C. catoirii* possède de faibles performances à la fois en situation de compétition et de non compétition. L'exclusion de *C. catoirii* reflète probablement une forme de maladaptation à un environnement largement modifié par l'Homme plutôt qu'une position le long d'un axe *r*-*K*. On peut supposer par exemple que cette espèce était adaptée antérieurement à des habitats forestiers relativement pauvres. Les différences entre les trois espèces invasives sont plus facilement interprétables dans le cadre *r*-*K*. Le principal contraste, à la fois en termes d'invasion dans la nature et de traits d'histoire de vie au laboratoire, existe entre *Bactrocera zonata* et les deux *Ceratitis* spp. Cette comparaison renforce l'idée que la possession de traits plus orientés *K* que ceux des espèces résidentes favorise l'invasion, même au prix d'un taux de croissance de la population plus faible en conditions optimales de non compétition.

Les stratégies démographiques en lien avec l'aptitude à la compétition ont également été comparés entre un biotype invasif et d'un biotype indigène de La Réunion chez l'aleurode *Bemisia tabaci* (Homoptera : Aleyrodidae) [P14]. Le biotype invasif semble avantagé sur le

résident en termes de rapidité de croissance démographique (taux d'accroissement naturel plus élevé) et en termes de compétition (taille des adultes et des œufs plus importante).

Plus généralement, la capacité à la compétition d'une espèce est toujours relative à un environnement local et à une communauté résidente. Lorsqu'on cherche à établir des généralités sur les invasions, on ne devrait pas mélanger les invasions primaires (en l'absence d'espèces résidentes apparentées) et secondaires (en présence d'espèces résidentes apparentées) (Facon *et al.*, 2006). En effet, lors des invasions secondaires, il semble plus approprié de considérer les différences entre les traits biologiques des envahisseurs et ceux de la communauté résidente que les valeurs absolues des traits des envahisseurs. Les résultats de cette étude ne sont donc pas en contradiction avec les méta-analyses concluant que les envahisseurs sont de stratégie *r* (Rejmanek & Richardson, 1996; Richardson & Rejmanek, 2004). En effet, les envahisseurs peuvent être à la fois de stratégie *r*, en comparaison avec les espèces non invasives, spécialement dans le cas des invasions primaires (où la colonisation peut être le facteur le plus limitant), et de stratégie *K* en comparaison avec les espèces apparentées de la communauté résidente, lorsque celles-ci sont présentes (invasion secondaire).

I.B.2) Coexistence entre espèces envahissantes et espèces résidentes via leur tolérance aux facteurs climatiques et aux plantes-hôtes

Publications P7, P12, P14, P16, P=article publié ; S=article soumis

Deux modèles extrêmes peuvent gouverner les invasions successives, avec un gradient continu entre les deux : (i) exclusion séquentielle : chaque nouvelle espèce introduite exclut les espèces préalablement établies ; (ii) coexistence cumulative (par exemple par séparation de la niche) : une nouvelle espèce occupe uniquement une partie de l'espace écologique, soit sans affecter les autres espèces, soit en diminuant une partie de leur répartition, mais en ne les conduisant pas à l'extinction. Les proportions relatives de ces deux modes vont déterminer la richesse spécifique de la communauté après les invasions. Parmi les invasions successives de bioagresseurs dans le monde, l'exclusion compétitive complète est rare, suggérant que les espèces résidentes persistent généralement dans des niches refuges. Du point de vue de la gestion des bioagresseurs, il est important de prévoir si les espèces successivement introduites sont capables de coexister.

Les espèces envahissantes modifient les communautés locales en formant de nouveaux réseaux d'interactions interspécifiques. L'émergence de nouvelles relations trophiques a souvent des conséquences spectaculaires sur les communautés indigènes, en particulier dans le cas d'introductions de prédateurs dans des îles isolées, initialement dépourvues de prédateurs (Fritts & Rodda, 1998). Cependant, les interactions compétitives et la différentiation de niche peuvent également être très importantes quand des espèces écologiquement et phylogénétiquement proches de l'envahisseur sont déjà présentes (Holway *et al.*, 2002; Reitz & Trumble, 2002). Ces situations sont intéressantes pour évaluer le rôle de la différentiation de niche dans l'assemblage des communautés, et de vérifier dans quelle mesure les expériences de laboratoire sur les axes de la niche peuvent être utilisés pour prédire quelles combinaisons d'espèces vont coexister.

L'étude de l'influence des facteurs climatiques sur le développement des Tephritidae de La Réunion montre que les espèces ont des niches fondamentales qui se chevauchent, et toutes les paires possibles d'espèces sont présentes en syntopie (à des fréquences variables) sur le terrain ; la compétition peut donc intervenir en nature [7]. Cependant, certains couples d'espèces ont des optima de développement assez différents et une différenciation de niche climatique peut ainsi avoir lieu. *Ceratitis rosa* peut se développer à des altitudes où le

développement des autres espèces ne peut avoir lieu. De la même façon, la tolérance à l'humidité et à la sécheresse de *C. capitata* et *C. rosa* est très différente, ce qui permet à ces deux espèces de coexister. Le fait que les niches climatiques de *C. capitata* et *C. catoirii* soient entièrement incluses dans celles des deux autres espèces plus compétitives, pourraient les conduire à terme à l'extinction.

Les facteurs climatiques peuvent donc promouvoir la coexistence à la suite d'une invasion et, plus largement, déterminer les effets des espèces invasives sur la composition des communautés après les invasions (Juliano & Lounibos, 2005). Des contrastes climatiques importants sont souvent rencontrés dans les îles océaniques jeunes comme La Réunion car le relief des îles volcaniques d'altitude élevée engendre des gradients d'altitude et des différences importantes de pluviosité entre les deux côtés des massifs montagneux (exposés aux vents dominants ou abrités). L'augmentation de la richesse spécifique des îles souvent observée à la suite des invasions (Sax *et al.*, 2002) peut être expliquée, en partie, par cette diversité climatique et la diversité des réponses à la température et à l'humidité des espèces. La possibilité de coexistence entre espèces indigènes et espèces exotiques est donc dépendante de la diversité du milieu considéré (Davies *et al.*, 2005). Plus celui-ci sera hétérogène et plus il y a de chances qu'une nouvelle espèce légèrement différente puisse trouver une partie de niche où la compétition est soit absente, soit à son avantage.

En ce qui concerne les plantes-hôtes, les quatre espèces de Tephritidae se chevauchent largement dans l'exploitation des fruits-hôtes [P12]. Cependant une espèce, *C. capitata*, semble capable d'exploiter des fruits non exploités par les autres. Si ces fruits sont suffisamment disponibles tout le long de l'année, ceci pourrait permettre la persistance à long terme de *C. capitata* en présence de *B. zonata*, espèce très compétitive dans une gamme climatique identique. On ne connaît pas de fruit où l'espèce endémique, *C. catoirii* se trouve dominante et cette espèce pourrait à terme être conduite à l'extinction.

La possibilité de coexistence entre deux biotypes de l'aleurode *Bemisia tabaci* a également été examinée en fonction de facteurs climatiques (température et pluviométrie) et de la gamme de plantes-hôtes [P14]. Il semble notamment que le biotype invasif B soit davantage associé aux plantes cultivées, alors que le biotype indigène Ms reste dominant sur les plantes indigènes et sous un climat particulier (humidité élevée). Il est suggéré que les biotypes invasifs sont caractérisés par des adaptations physiologiques, morphologiques et biologiques aux environnements perturbés créés par les activités humaines à différents endroits du monde, alors que les biotypes résidents peuvent persister dans les habitats moins altérés.

L'hypothèse de partage de niche par les plantes-hôtes a également été testée chez 6 espèces de nématodes phytophages ravageurs du bananier en Martinique [P16]. Les plantes-hôtes présentes dans les agroécosystèmes à base de bananiers ont une influence marquée sur la structure de la communauté de nématodes. Celles-ci permettent une partition de niche entre certaines espèces de la communauté. Cette séparation de niche est la plus marquée pour 3 espèces de nématodes considérées comme établies depuis longtemps sur la Martinique, ce qui est en accord avec le fait que ces espèces ont probablement été en contact pendant une longue durée et ont pu co-évoluer. Au contraire, il y a peu de potentiel pour une partition de niche entre les espèces envahissantes récentes (*Radopholus similis* et *Helicotylenchus multicinctus*). D'un point de vue appliqué, la modification de l'abondance de certaines plantes-hôtes, qui peuvent être utilisées comme plantes de couverture entre les rangs ou pendant la jachère, peut modifier l'équilibre entre les différentes espèces. Pour les espèces ne présentant pas de partition de niche *via* les plantes-hôtes, des études sur la colonisation et la dynamique des populations dans le temps, à la fois à l'échelle de la racine et de l'agroécosystème, permettraient d'améliorer notre compréhension des équilibres entre espèces dans cette communauté.

II – Perspectives

Dans un premier temps, les thématiques présentées précédemment concernant la biodémographie et les interactions entre espèces seront poursuivies sur le charançon du bananier *Cosmopolites sordidus* et la communauté de nématodes phytophages des bananeraies. Les traits de vie de *C. sordidus* seront étudiés au laboratoire afin de mieux comprendre sa stratégie démographique et sa dispersion. La compétition interspécifique entre les 6 espèces de nématodes phytophages sera étudiée afin d'améliorer la compréhension et la modification possible des équilibres entre les espèces de cette communauté.

Deux nouveaux projets de recherche sont proposés ci-après : le premier porte sur la caractérisation de l'habitat des bioagresseurs et la dynamique des populations en milieux hétérogènes, projet dans lequel s'inscrit une partie de la thèse de Fabrice Vinatier. Le deuxième projet porte sur les réseaux trophiques et leur modification par les pratiques culturales dans l'agroécosystème, projet dans lequel s'inscrit la thèse de Grégory Mollot.

II.A) Caractérisation de l'habitat des bioagresseurs, dynamique et dispersion des populations en milieux hétérogènes.

Publications: P15, S3, S4; P=article publié ; S=article soumis

Alors que le concept de niche écologique établit le lien entre une gamme de variable environnementale et la valeur adaptative ou *fitness* de l'espèce, la caractérisation de l'habitat s'intéresse au lien entre ces variables environnementales et la probabilité d'occurrence de cette espèce (Hirzel & Le Lay, 2008). En l'absence d'immigration, une espèce peut subsister uniquement si la combinaison locale des variables environnementales permet un taux d'accroissement naturel positif. La niche écologique est un volume à *n* dimensions, représentées par ces variables, dans l'espace environnemental permettant une croissance positive (Hutchinson, 1957). La diminution du taux d'accroissement naturel de l'optimum de la niche à l'enveloppe où il devient nul (Tilman, 1980) définit la forme de la niche. Au-delà, le taux d'accroissement naturel devient négatif.

La présence d'une espèce dans un endroit donné obéit à trois types de contraintes (Soberon & Nakamura, 2009) : (i) l'environnement local doit permettre la croissance de la population (Grinnell, 1917), (ii) les interactions avec les autres espèces locales (prédation, compétition, etc…) doivent permettre à l'espèce de persister (Elton, 1927), et (iii) l'endroit doit être réellement accessible, considérant la capacité à la dispersion de l'espèce. Ces contraintes déterminent la distribution géographique de l'espèce. Il est donc théoriquement possible de reconstruire une niche de Grinnell pour une espèce à partir des variables environnementales mesurées à l'endroit qu'elle occupe. Cette reconstruction et les prédictions spatiales qui en dérivent sont les objectifs des modèles de caractérisation de l'habitat (Hirzel & Le Lay, 2008). En pratique, l'importance du lien entre distribution et niche dépend de l'écologie de l'espèce, des contraintes locales et des événements historiques.

Les facteurs déterminant la distribution spatiale du charançon et des nématodes du bananier sont encore peu connus. Par contre, il existe des données sur la présence et l'abondance de ces espèces dans différentes zones de la Martinique. Depuis mon affectation en Martinique, je me suis attaché à rassembler ces données diverses pour en constituer des bases utilisables pour des analyses écologiques sur la caractérisation de leur habitat et des facteurs modulant la dynamique de leurs populations. Les données collectées concernent le charançon du bananier *Cosmopolites sordidus* entre 2003 et 2008 (environ 40 000 lignes de données) et six espèces de nématodes phytophages présents en bananeraie (*Radopholus*

similis, Pratylenchus spp., Meloidogyne spp. Helicotylenchus spp., Hoplolaimus seinhorstii, Rotylenchulus reniformis) entre 2002 et 2008 (environ 3000 fiches provenant du laboratoire de nématologie du PRAM ont été saisies). Les données comprennent les abondances pour les différentes espèces, les coordonnées géographiques, les dates de prélèvement, les dates de plantation, différentes variables environnementales (température, pluviosité, type de sol) et pratiques culturales (précédent cultural, présence et type de jachère, …). Les données étant géolocalisées, il sera possible de les compléter par d'autres couches de données provenant de systèmes d'information géographiques (SIG). Ces bases pourront être analysées par différentes méthodes statistiques avancées (Calenge & Basille, 2008; Calenge *et al.*, 2008; Hirzel & Le Lay, 2008) afin de mettre en évidence les grands facteurs déterminant l'habitat des différentes espèces. Ils serviront également à valider les résultats sur les capacités de dispersion des espèces [S3] ou les simulations des modèles mécanistes mis au point.

Grâce à une partie de ces données collectées pour lesquelles on possède une maille fine (> 16 pièges. ha^{-1}), l'effet de l'hétérogénéité spatiale sera ensuite étudié sur les populations de *C. sordidus.* Une revue des méthodes disponibles pour mettre en évidence les facteurs et mécanismes expliquant l'hétérogénéité spatiale [S4] a été réalisée par Fabrice Vinatier, doctorant pour lequel je participe à l'encadrement. Un premier objectif est de définir le type d'organisation spatiale des populations. Différentes analyses géostatistiques sont adaptées en fonction des procédures d'échantillonnage. Un modèle mécaniste peut ensuite être réalisé pour représenter les mécanismes sous-jacents à l'organisation spatiale décrite. Nous avons recensé les différents mécanismes possibles incluant la dispersion, l'interaction entre les individus, les facteurs affectant la dispersion et leurs interactions, et la façon dont ils sont représentés dans les modèles de métapopulation, les modèles individu-centrés et les modèles d'automate cellulaire. L'explication de l'hétérogénéité spatiale des insectes peut bénéficier d'une combinaison d'approches statistiques et d'approches de modélisation mécanistes ; par exemple, les modèles statistiques spatiaux facilitent les tests d'hypothèse sur les mécanismes d'hétérogénéité spatiale. Cependant les études combinant les deux types d'approche sont rares. Fabrice Vinatier a développé un modèle spatialement explicite capable de simuler l'épidémiologie de *C. sordidus* [P15]. Le modèle est basé sur le déplacement local des adultes et les traits de vie de base (fécondité, développement larvaire, mortalité, …). Ce modèle a été utilisé pour tester différents arrangement spatiaux de bananiers, sur l'épidémiologie du ravageur. Ce modèle servira également à tester des ressources hétérogènes réparties dans l'espace, comme des mosaïques de variétés ayant des sensibilités différentes.

II.B) Comment les réseaux trophiques des bioagresseurs sont t-il modifiés par les pratiques culturales ?

Publications: S1, S2; P=article publié ; S=article soumis

Les différentes espèces des réseaux trophiques des agroécosystèmes, en particulier les prédateurs généralistes, peuvent jouer un rôle important dans le contrôle des bioagresseurs (Carter & Rypstra, 1995; Cardinale *et al.*, 2003; Costamagna *et al.*, 2007). L'objectif de ce projet est de comprendre comment les populations du charançon du bananier, *Cosmopolites sordidus*, sont régulées par des facteurs biotiques. Abera-Kalibata *et al.* (2007) ont montré le potentiel important de la régulation des populations de *C. sordidus* par des prédateurs généralistes. Ce potentiel de régulation est dépendant de la structure des réseaux trophiques qui peut être modifiée par différentes pratiques agricoles, tel que l'ajout de plantes de couverture, et plus généralement par le niveau d'intensification de la culture. Le couple bananier/charançon constitue un modèle biologique intéressant pour ce projet car i) le bananier est une plante semi-pérenne permettant d'atteindre rapidement un pseudo-climax, et

ii) le charançon est un bioagresseur ayant une dispersion spatiale réduite, limitant ainsi les effets de confusion entre dispersion et régulation.

La thèse de Grégory Mollot (2009-2012), dont je suis l'encadrant principal et se déroulant au PRAM (Martinique) fait partie intégrante de ce projet.

Dans une première étude réalisée au PRAM [S1], nous avons évalué l'effet de l'ajout d'une plante de couverture, *Brachiaria decumbens*, sur la structure du réseau trophique dans une bananeraie, en analysant les variations en isotope stable du carbone et de l'azote pour *C. sordidus*, et ses prédateurs potentiels (araignées, fourmis, scolopendres et forficules). L'ajout de plante de couverture ne modifie pas la niche trophique du charançon, indiquant l'absence d'effet *bottom up* de *B. decumbens* sur les populations de *C. sordidus*. Au contraire, l'ajout de la plante de couverture modifie la position trophique (indiquée par la signature en $\delta^{13}C$) des prédateurs généralistes. La plante de couverture, *B. decumbens*, forme une nouvelle ressource pour une communauté plus diverse d'insectes herbivores, ceux-ci constituant une ressource alternative pour les prédateurs généralistes. La plante de couverture peut donc potentiellement favoriser les populations de prédateurs et donc participer à la régulation du bioagresseur. Cette hypothèse de régulation doit être vérifiée dans les études futures.

Dans ce projet nous testerons les deux hypothèses suivantes : (i) les pratiques culturales modifient la structure et la stabilité des réseaux trophiques ; et (ii) la structure des réseaux trophiques agit sur le potentiel de régulation du charançon, par des mécanismes tels que contrôle *top-down* et *bottom-up*, et prédation intra-guilde.

Le travail consistera à comprendre et à mesurer la régulation du charançon par les différentes espèces de la communauté (ressources, compétiteurs, prédateurs), puis d'estimer l'influence de la diversité spécifique de l'agrosystème, de son organisation spatiale, et plus généralement des pratiques culturales, sur cette régulation. Les mécanismes de régulation seront étudiés à trois niveaux : (i) au champ par des mesures d'abondance et isotopiques ($\delta^{15}N$ & $\delta^{13}C$) des taxa visant à identifier les espèces régulatrices et les liens trophiques. En effet, les isotopes du carbone et de l'azote permettent de connaitre l'origine de la ressource et le niveau trophique (Vander Zanden & Rasmussen, 1999). En outre, ces analyses, couplées à des modèles basés sur la signature isotopique des sources (Phillips & Gregg, 2003), peuvent permettre d'identifier les taxa ayant un rôle clef dans l'écosystème (Coat *et al.*, 2009). (ii) Les liens trophiques entre le charançon et certaines espèces ciblées dans le premier point seront confirmés au laboratoire. L'importance de la consommation des ressources, de la compétition et de la prédation sera estimée au laboratoire. (iii) Les connaissances acquises dans les deux premiers points seront intégrées dans un modèle de simulation du réseau trophique, permettant de quantifier ces régulations et de les optimiser pour proposer des concepts de systèmes de culture plus durables.

A terme, ce projet de recherche inclut également la construction d'un modèle de fonctionnement d'agroécosystème permettant de simuler les liens entre sol, plantes et réseaux trophiques [S2]. En effet la modélisation des agroécosystèmes pourrait davantage prendre en compte les concepts d'écologie, tel que celui de réseau trophique. Un nombre croissant d'écosystèmes est manipulé pour l'agriculture ou la conservation (Tilman *et al.*, 2002) et leurs fonctions écologiques ont besoin d'être maintenues (Cardinale *et al.*, 2006). Il est nécessaire de simuler le fonctionnement des systèmes agricoles afin d'aider à la conception de nouveaux agroécosystèmes productifs et durables basés sur des processus écologiques de régulation au lieu de produits chimiques externes. Les structures des réseaux trophiques des agroécosystèmes affectent énormément leur performance agronomique et leur stabilité (Neutel *et al.*, 2007). Bien qu'il ait été reconnu depuis longtemps que les communautés sous-

terraines et aériennes sont impliquées dans les fonctions basiques des agroécosystèmes, leur action a souvent été ignorée en agronomie. En simulant les systèmes agricoles, les agronomes se focalisent souvent sur le continuum sol-plante-atmosphère (Jones *et al.*, 2003). Les modèles de réseaux trophiques pourraient ainsi être liés aux modèles sol-plante. Pour ce faire, les futures études doivent inclure les propriétés émergentes des agroécosystèmes, comme les interactions entre les communautés sous-terraines et aériennes, le contrôle des bioagresseurs par le biais des chaines trophiques, et les répercussions positives sur les propriétés des sols.

Ce projet s'inscrit dans l'axe prioritaire 1 du CIRAD « Intensification écologique ». En effet la compréhension des processus écologiques de la régulation des bioagresseurs est un enjeu majeur pour élaborer des systèmes de culture économes en intrants (produits chimiques, énergie) et moins générateurs d'effets négatifs pour l'environnement. Le pilotage des systèmes vivants nécessite de comprendre et de mesurer les interactions entre les espèces présentes dans les agroécosystèmes.

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COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields

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ABSTRACT

A stochastic individual-based model called COSMOS was developed to simulate the epidemiology of banana weevil *Cosmopolites sordidus*, a major pest of banana fields. The model is based on simple rules of local movement of adults, egg laying of females, development and mortality, and infestation of larvae inside the banana plants. The biological parameters were estimated from the literature, and the model was validated at the small-plot scale. Simulated and observed distributions of attacks were similar except for five plots out of 18, using a Kolmogorov–Smirnov test. These exceptions may be explained by variation in predation of eggs and measurement error. An exhaustive sensitivity analysis using the Morris method showed that predation rate of eggs, demographic parameters of adults and mortality rate of larvae were the most influential parameters. COSMOS was therefore used to test different spatial arrangements of banana plants on the epidemiology of *C. sordidus*. Planting bananas in groups increased the time required to colonise plots but also the percentage of banana plants with severe attacks. Spatial heterogeneity of banana stages had no effect on time required to colonise plots but increased the mean level of attacks. Our model helps explain key factors of population dynamics and the epidemiology of this tropical pest.

1. Introduction

Understanding the epidemiology of pests is of special importance for better management (Zadoks and Schein, 1979; Madden, 2006). The spatial component of epidemiology is a crucial element in the spread of damages from a localised inoculum or when pest dispersal is limited (Winkler and Heinken, 2007). Fecundity, mortality, and dispersal are the driving forces of insect epidemiology (Schowalter, 2006, p. 137). Pests can disperse heterogeneously (Lopes et al., 2007). The dispersal behaviour of mobile stages between each host plant contributes greatly to explaining variations of local densities of the species (Coombs and Rodriguez, 2007). In tropical and subtropical regions, where populations of plants and pests are not synchronised by severe winters, all stages of most insects are present simultaneously (Godfray and Hassell, 1987). In these conditions, all stages should be considered simultaneously to understand the distribution and abundance of organisms in the field. This approach is different from the ones in temperate regions, which focus on a particular part of the life cycle of insects that is considered as a key point of spatial patterning and demography, such as attacks or dispersal behaviour of adults (e.g. Cain, 1985; Brewster et al., 1997), egg laying of females (Zu Dohna, 2006), or post-embryonic stages (egg or larva) (e.g. Johnson et al., 2007).

In this work, we took as case study the banana weevil *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar. 1825), a major pest of banana cropping systems. Larvae bore into the corm of banana plants and damage the points of insertion of primary roots, leading to plant snapping and toppling (Montellano, 1954; Gold et al., 2001). *C. sordidus* can contaminate new banana plantations through infested planting material or by means of adults that have survived since the last banana planting, because it has a long development time and life span, a low mortality rate, and is able to survive without food for extended periods (2–6 months) in moist environments (Gold et al., 2001). Adult weevils, which have limited dispersal abilities, can also invade new plantations from nearby plantations or from fallows when heavily infested banana plots are transformed into fallows (Gold et al., 2001). Banana plant stages may be heterogeneous in a plot, because plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner, 1994). This spatial heterogeneity of banana plant stages is likely to

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influence weevil population dynamics because of the influence of banana stage on female egg laying (Cuillé, 1950; Vilardebo, 1973). Based on these characteristics, we chose (i) a spatially explicit approach to understand how local movements influence the spatial distribution and damages of this pest in relation to its habitat and (ii) an individual-based modeling (IBM) approach to help explain observed population patterns (Winkler and Heinken, 2007), considering that different behaviours at the individual level can lead to the emergence of population-level properties (Grimm and Railsback, 2005). Modeling was considered as a good means to implement these approaches and an IBM was chosen as the modeling framework.

In this paper, we present the COSMOS model, aimed at simulating the spatial epidemiology of *C. sordidus* in the long-term by describing its population dynamics and the resulting infestation of host plants. The model considers all insect stages simultaneously and assumes there are individual variations in behaviour according to each developmental stage. We hypothesised that the distribution of *C. sordidus* populations and attacks in banana fields can be modelled according to epidemiological rules identified at an individual level and calibrated from the literature, with a model that is less parameter-demanding than most IBMs. The COSMOS model, like many IBMs, aims at bridging the gap between individual behavioural ecology and population dynamics (De Angelis and Gross, 1992). We validated COSMOS by comparing model outputs with field data, which is rarely done with most IBMs (Alderman and Hinsley, 2007; Charnell, 2008). Then, because sensitivity analyses are key steps of the modelling processes (Parry et al., 2006; Arrignon et al., 2007), we first conducted an exhaustive sensitivity analysis using the Morris method (Morris, 1991) to identify the most influential parameters in our model. In a second step, these parameters were studied in detail on an extended range of variation, including extreme values. Finally, we used COSMOS to test how planting patterns and the spatial heterogeneity of plant stages, resulting from the variability of sucker appearance over cropping cycles, could modify the time necessary to colonise the whole plot and the level of damage during three cropping cycles, when the initial weevil population was distributed along one side of the plantation.

2. Model description and parameterisation

2.1. General features of the COSMOS model

The COSMOS model is a stochastic IBM that runs on a daily time step. It simulates the local movement and egg laying of females in the field, infestation of larvae in banana plants, and the main features of insect and host plant development (Fig. 1). According to the model, individual *C. sordidus* disperse in a field that is represented by a grid with one banana plant per cell (grid area ranged between 144 and 441 m^2). Plants pass through three distinct stages until harvest: maiden sucker, preflowering, post-flowering. Just before flowering, a new sucker of the mother plant is selected that grows simultaneously in the same cell. The time lag between two consecutive harvests, corresponding to a cropping cycle, is about 200 days (see Tixier et al. (2004) for details on banana cropping cycles).

C. sordidus females lay eggs on banana plants, and larvae issued from these eggs bore into the corm of the plants. The stage duration of juveniles and the phenologic stages of banana plants are temperature-dependent. In the COSMOS model, each *C. sordidus* is an autonomous individual that has a set of rules for egg laying and movement behaviour, depending on the plant stage at the insect's current position. Males do not cause damage, and no data are available on the influence of mating on egg laying. Therefore, males were excluded from the model.

A rule is an algorithm specified by the modeller to define a behaviour of individuals (Grimm and Railsback, 2005). The platform used to develop the model was the CORMAS (Common-pool Resource and Multi-Agents System) software (Bousquet et al. (1998); see http://cormas.cirad.fr), which is based on the Smalltalk object-oriented language (Visual Works 7.5, Cincom Softwares). The architecture of the model was developed in accordance with Ginot et al. (2002). Table 1 presents all the model parameters described below and their estimated values.

2.2. Dispersion

Eggs, larvae, and pupae cannot disperse between banana plants, and adults disperse slowly by crawling (Gold et al., 2001). Although the banana weevil has functional wings, most observers have reported that the weevil seldom, if ever, flies (Gold et al., 2001). In banana fields planted in monoculture (1500–2200 plants/ha, with standard planting distances of 2.4 m × 2.4 m), individuals do not search for food in a large area; their behaviour rather corresponds to an area-restricted search response type (Morris and Kareiva, 1991). The proportion of individuals that disperse to a given banana plant can be estimated as a negative exponential function of the distance to the plant (Schowalter, 2006). Adjusting the data of Delattre (1980) and Gold et al. (2001) to such a function, the probability (P) each time step of an adult moving to a given banana plant at distance d (in m) is the following (Eq. (1)):

$$P = 0.06\, e^{-0.62\, d} \quad (1)$$

2.3. Egg laying and longevity of adults

Once inseminated, *C. sordidus* females can stay gravid for 15 months without renewed mating (Cuillé, 1950; Treverrow et al., 1992). Authors disagree on the possible effect of age on egg laying (Gold et al., 2001). Yet it is agreed that egg laying depends mainly on two processes. First, egg laying probability and fecundity increase over banana phenologic stages (Cuillé, 1950; Vilardebo, 1973); the maximal probability of egg laying and fecundity occurs at the post-flowering stage, see Table 1 (Koppenhofer, 1993; Abera-Kalibata et al., 1999). Second, egg laying activity declines when the number of adults per plant increases (Cuillé, 1950; Koppenhofer, 1993; Abera-Kalibata et al., 1999).

In our model, mating and the effect of age on egg laying are not considered. Egg laying occurs for each female once a week, according to the period found in the literature (Koppenhofer, 1993), and follows a binomial distribution with a probability depending on the stage of the host plant (flowering, preflowering and maiden sucker) as estimated by Abera-Kalibata et al. (1999). If conditions for egg laying are fulfilled, the fecundity of each female is assumed to be Poisson-distributed (in accordance with Hilker et al. (2006)), with parameter equal to 2.7 if the adult density exceeds a given threshold (*DE*, Table 1) and 0.8 otherwise.

The maximal lifespan of adult of *C. sordidus* was estimated to be 748 days (Froggatt, 1925; Gold et al., 2001). The mortality rate of adults is often considered as constant during their lifespan (Godfray and Hassell, 1989; Berec, 2002; Potting et al., 2005). To our knowledge, no data are available on the predation rate of *C. sordidus* adults in the field.

Following Bousquet et al. (2001), *MR* was calculated assuming a discrete decreasing process, as a function of the maximum lifespan (*ML*, in days, Table 1; Eq. (2)). We assumed a high mortality rate (0.99) of adults from emergence to the maximum lifespan and a constant daily mortality (*MR*). The shape of the survival schedule exponentially decreases in those conditions and is convex (Carey,

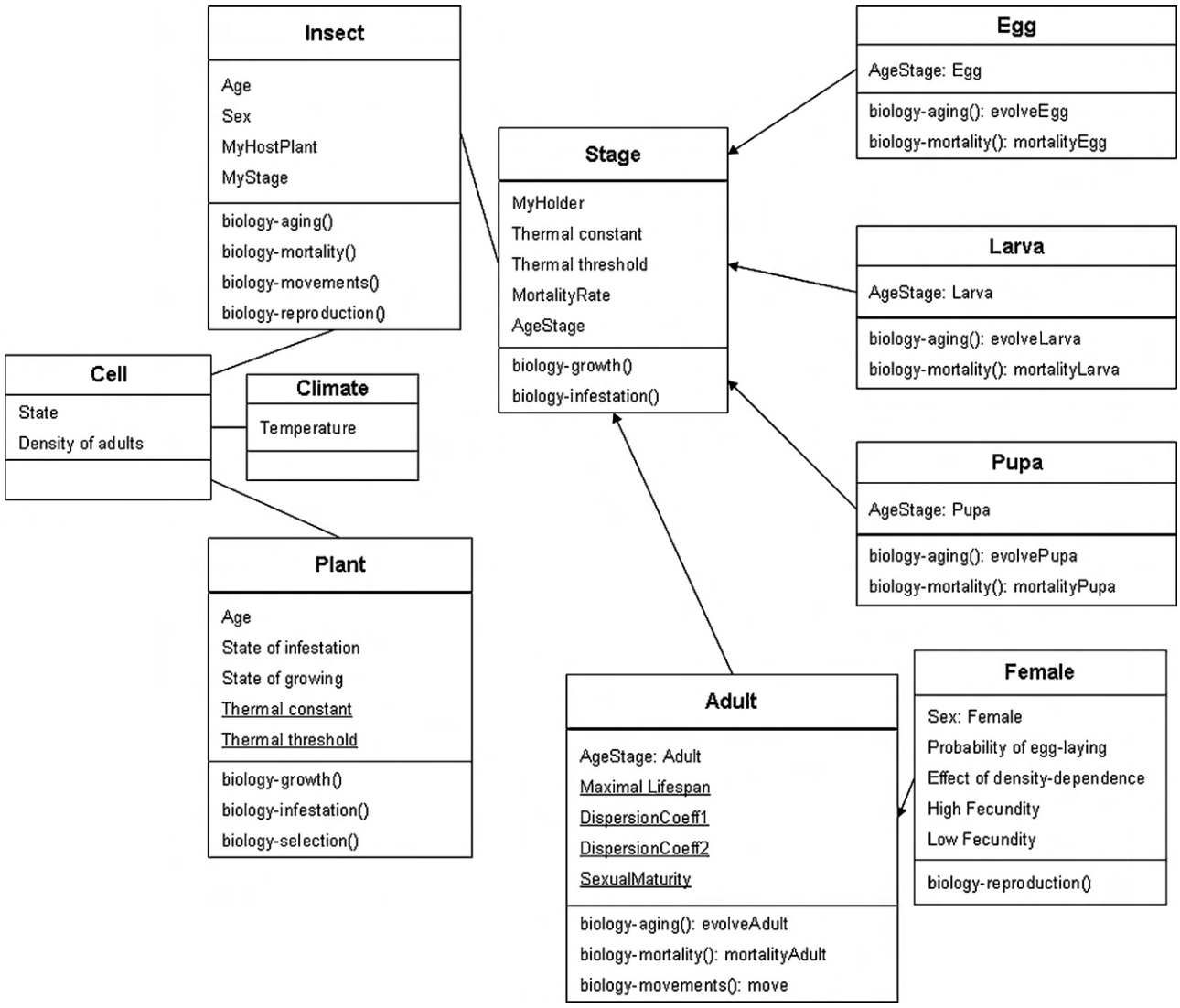

Fig. 1. Static structure of the spatially explicit model COSMOS in Unified Modeling Language (UML). Each box contains the name of a class in the first part, its key attributes in the second part, and the rules in the third part. For example, an individual of class Adult moves according to the rule biology-movements ( ) and the key attributes DispersionCoeff1 and DispersionCoeff2. Class attributes are shared for all the individuals of the class (underlined names) and instance attributes have a specific value for each instance (non-underlined names). Arrows between boxes signify inheritance, and simple links signify association. For example, an individual of class Adult inherits from class Stage and is associated with class Insect.

2001):

$$MR = 1 - (0.01)^{1/ML} \quad (2)$$

2.4. Development and mortality of immature stages

The development of *C. sordidus* is driven by temperature (Kiggundu et al., 2003a). Eggs, larvae, and pupae have different intrinsic mortality rates; larvae are the most susceptible stage (Traore et al., 1993, 1996; Kiggundu et al., 2003b). However, eggs laid on the surface of the corm are exposed to additional mortality by predators, e.g. ants (Koppenhofer, 1993; Abera-Kalibata et al., 2007, 2008). Mortality rates of immatures and additional mortality resulting from predators are shown in Table 1.

In the model, the physiological age for each juvenile stage i increases each day, at a rate determined by the difference between the daily temperature and a thermal threshold corresponding to stage i. Daily temperature was calculated as the mean between minimum and maximum temperature. Table 1 presents the thermal constants, i.e. the number of degree-days above the thermal threshold required to complete development from stage i to the $i+1$th stage. Mortality at stage i follows a binomial distribution based on a constant mortality rate, because the literature gives only cumulative mortality rates at the end of each stage.

2.5. Development of banana plants

The thermal threshold for banana-plant development was estimated to be 14 °C (Ganry, 1980), and the duration in degree-days of each stage from planting to harvesting was determined by Abera-Kalibata (1997) and Tixier et al. (2004) (Table 1). In the COSMOS model, flowering rate follows a normal distribution (mean = 2350 degree-days; σ = 200 degree-days), adapted from Tixier et al. (2004). The sucker of the following cycle is selected after 2180 degree-days (Tixier et al., 2004).

2.6. Infestation of banana plants

Damage resulting from adult *C. sordidus* feeding is negligible compared to that resulting from larvae (Gold et al., 2001). When

Table 1
Model parameters, their values and ranges for sensitivity analyses, and corresponding references.

Description	Code	Value	Range used for the first sensitivity analysis	References
Egg				
Thermal constant to reach next stage (degree-days)	TCE	89	80.1–97.9	Gold et al. (2001)
Thermal threshold for development (°C)	TTE	12	10.8–13.2	Gold et al. (2001)
Mortality rate for eggs	MRE	0.11	0.09–0.12	Kiggundu et al. (2003a,b)
Proportion of eggs removed by predators	PE	0.6	0.33–0.68	Koppenhofer (1993) and Abera-Kalibata et al. (2008)
Larva				
Thermal constant to reach next stage (degree-days)	TCL	537.9	484.1–591.7	Traore et al. (1996)
Thermal threshold for development (°C)	TTL	8.8	7.9–9.7	Traore et al. (1996)
Mortality rate for larvae	MRL	0.48	0.32–0.64	Kiggundu et al. (2003a,b)
Diameter of gallery (in cm)	G	1	0.8–1.2	Montellano (1954) and Sponagel et al. (1995)
Pupa				
Thermal constant to reach next stage (degree-days)	TCP	120.7	108.6–132.8	Traore et al. (1996)
Thermal threshold for development (°C)	TTP	10.1	9.09–11.11	Traore et al. (1996)
Mortality rate for pupae	MRP	0.18	0.095–0.265	Traore et al. (1996)
Adult				
Sex-ratio (male:female)	–	1:1	–	Gold et al. (2001)
Sexual maturity for females after emergence (days)	SM	34.5	33–36	Cuillé (1950)
Probability of egg-laying on maiden sucker compared to flowered plants	OPMS	0.11	0.08–0.13	Estimated from Abera-Kalibata (1997)
Probability of egg-laying on preflowered plants compared to flowered plants	OPPF	0.41	0.39–0.46	Estimated from Abera-Kalibata (1997)
Number of adults per week necessary for density-dependent effect on fecundity	DE	20	10–33	Abera-Kalibata (1997)
Number of eggs per week per female without density-dependent effect	FH	2.7	1.7–3.2	Koppenhofer (1993)
Number of eggs per week per female with density-dependent effect	FL	0.8	0.6–1.1	Koppenhofer (1993)
Proportion of individuals moving 2 m per time step (%)	DC1	1.4	1.5–6.6	Delattre (1980)
Proportion of individuals moving 4 m per time step (%)	DC2	0.3	0.0–3.0	Delattre (1980)
Maximum lifespan of adult (days)	ML	748	520–900	Estimated from Froggatt (1925)
Banana plant				
Interval planting–maiden sucker (degree-days)	–	800	–	Estimated from Abera-Kalibata (1997)
Interval planting–preflowering (degree-days)		1600		Estimated from Abera-Kalibata (1997)
Interval planting–post-flowering (degree-days)		2350		Tixier et al. (2004)
Standard deviation for flowering rate (degree-days)		200		Adapted from Tixier et al. (2004)
Appearance of first sucker (degree-days)		2180		Tixier et al. (2004)
Interval planting–harvesting (degree-days)		3250		Tixier et al. (2004)
Thermal threshold (°C)		14		Ganry (1980)
Maximal circumference of plant at harvesting (cm)		60		

larvae are ready to pupate, they burrow toward the outer surface of the corm (Froggatt, 1925). The attacked circumference (*AC*), measured at the outer surface of the corm of each banana plant, is a common indicator of damage; it is assumed to be proportional to the number of galleries bored by the larvae. When the whole circumference of the corm is attacked, eggs and larvae die because of resource limitation (Koppenhofer and Seshu Reddy, 1994).

In the model, at each time step, the attacked circumference (*AC*) is estimated as the total number of larvae that have reached emergence multiplied by the mean diameter of a gallery (i.e. 1 cm according to Montellano (1954) and Sponagel et al. (1995)). The maximum value of *AC* is equal to the maximum circumference of the banana plant at harvest.

3. Materials and methods

3.1. Field data

Damages of *C. sordidus* on banana plants were measured on 18 plots during two cropping cycles at the CIRAD experimental station,

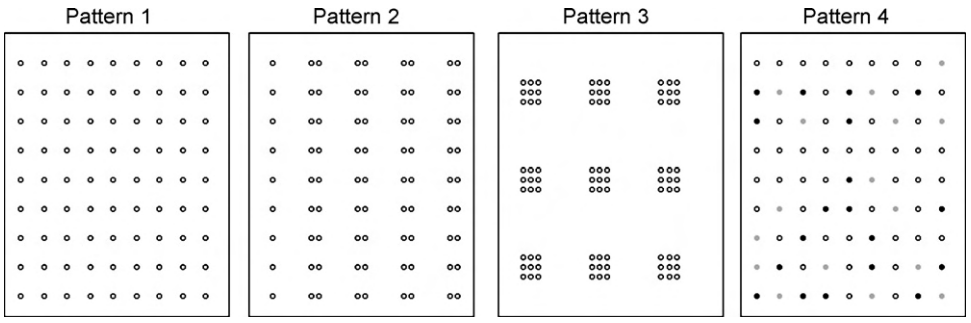

Fig. 2. Spatial arrangements of banana plants used in simulations: regular planting (1), double row planting (2), patch planting (3), regular planting with heterogeneity of banana stages (4). Color gradation figures from white to black the different banana stages from the youngest to the oldest, respectively. Planting density is 1750 plants/ha everywhere.

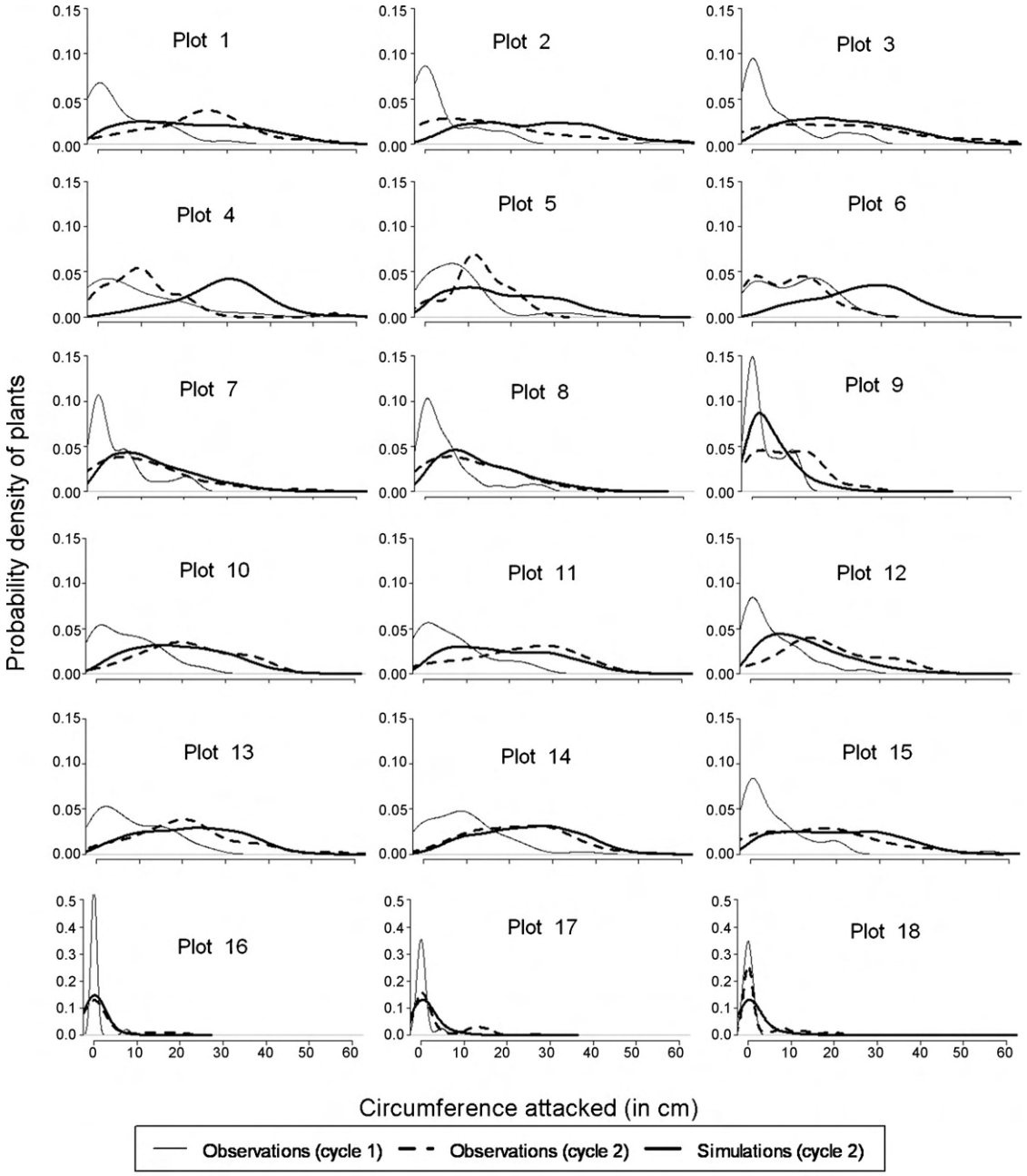

Fig. 3. Observed and simulated distribution of banana damages in 18 plots infested by *Cosmopolites sordidus* in Guadeloupe. Distributions are depicted by probability densities. Simulated probability densities were obtained over 100 runs for each plot. The solid thin line represents the distribution of attacks at the end of the first cycle (initialization). Bold lines represent the observed (dotted) and simulated (solid) distributions. Note that *y*-scale is different for plots 16–17–18.

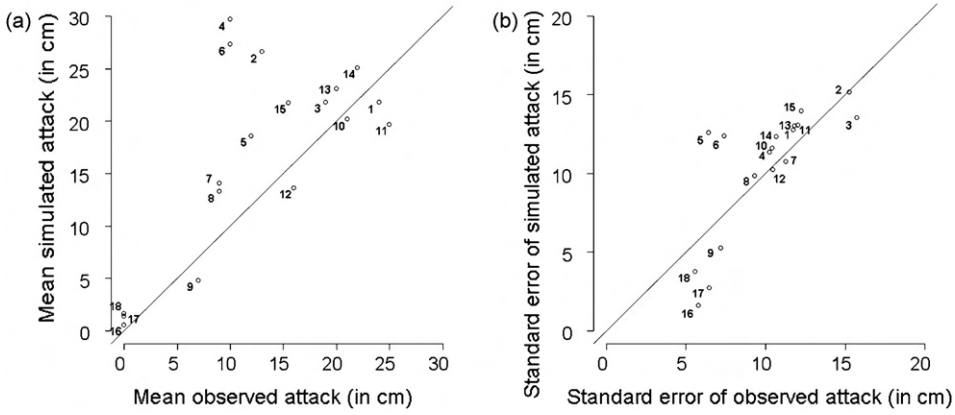

Fig. 4. Comparison of observed vs. simulated (a) mean and (b) standard deviation of distributions for each plot. Solid line indicates a perfect fit between observation and simulation. Numbers correspond to plot numbers.

Neufchâteau, Guadeloupe (French West Indies, 16°15′N, 61°32′W, altitude 250 m) between 1990 and 1995. The plots contained 30–42 banana plants (2174 plants/ha, *Musa* spp., AAA group cv. Cavendish Grande Naine) and were separated by a row without plants. Initial inoculums of *C. sordidus* arrived from previous banana crops. At each harvest, damages caused by larvae inside the corm were evaluated on each banana plant by removing 10 cm of topsoil around the corm and a band of tissue 7 cm wide and 0.5 cm deep across the corm at its widest point. The circumference of the corm with galleries was measured using a tape measure.

3.2. Simulation procedures

3.2.1. Model validation

The simulation area was a 15 × 15 to 18 × 21 cell grid (cell dimension: 0.8 m × 0.8 m), according to the number of banana plants in each field. Each banana plant belonged to one cell and was separated from other plants by two empty cells. Simulations were run over 200 days, corresponding to the period between two consecutive harvests. Model inputs consisted of daily mean temperature from a five-year dataset and of initial populations (see below). Because of the model stochasticity, we performed 100 replicates for each situation and averaged the results.

For each of the 18 plots used for model validation, the model was initialised using populations of individuals distributed in the plot, estimated according to the attacks recorded at the end of the first cycle for each plant, i.e. the attacked circumference (*AC*). For this estimation, we first established a relation to calculate the number of adults per plant from *AC* using data from a capture-recapture study performed in a banana field in Neufchâteau (1996–1997). In this study, populations had been trapped using pseudostem traps (Gold et al., 2002), and *AC* had been measured for each banana plant. The ratio of the abundance of *C. sordidus* adults (square-root-transformed to stabilise the variance) to *AC* was 0.22 ± 0.07 ($F = 18.85$; $P < 0.01$; df = 50). Having calculated the number of adults at the end of the first cropping cycle in each cell of the 18 grids by

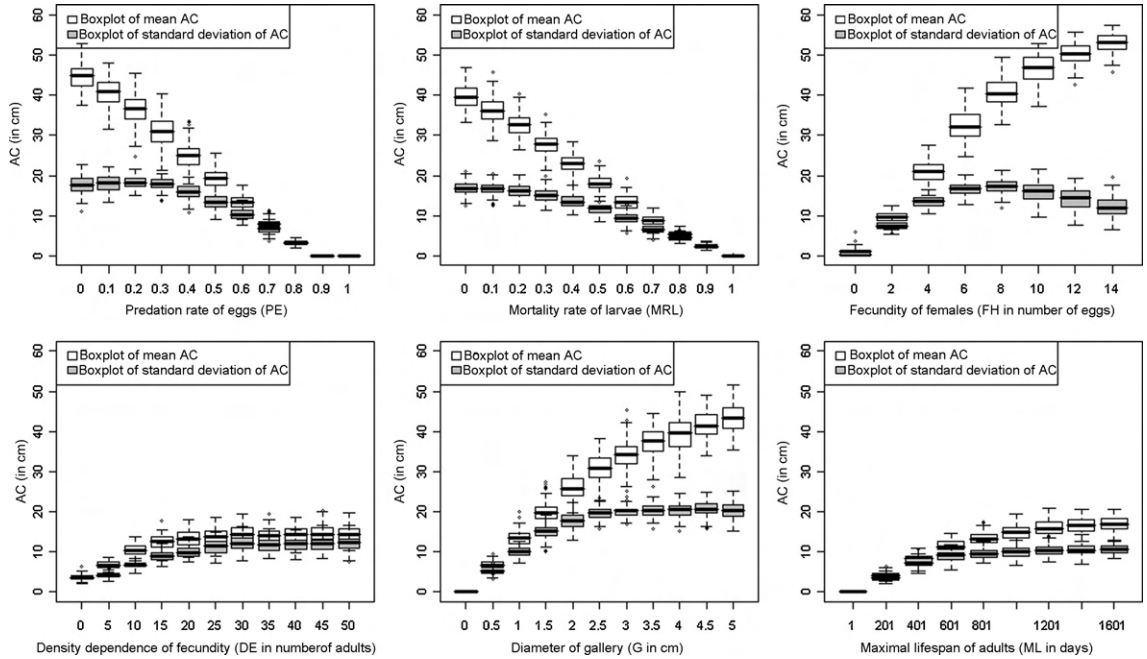

Fig. 5. Analyses of the COSMOS model sensitivity to the most influent insect biological parameters, focusing on two main parameters of the distribution of attacks on plot 8: mean (white boxes), standard deviation (grey boxes). A range of values was tested for each parameter, the other parameters being held constant. The output of 100 runs was computed in a boxplot. Each boxplot contains the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker. The whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box.

using this ratio, we set the population age structure, using ratios of 0.24, 0.48, 0.10, and 0.18 for egg, larvae, pupae, and adults, respectively (Koppenhofer, 1993). Within each stage the age was considered to follow a uniform distribution. Then, the model simulated the epidemiology of *C. sordidus* during the second cropping cycle.

3.2.2. Simulation of spatial arrangements of banana plants

We simulated different spatial arrangements of banana plants thought to have an effect on the time necessary for *C. sordidus* to colonise a plot and to cause damage. First, we simulated three planting patterns with synchronous banana stages (Fig. 2): (1) regular planting (2.4 m × 2.4 m), (2) double row planting (0.8 or 4 m × 2.4 m) and (3) patches of nine banana plants (5.6 m × 5.6 m between each patch). The age of banana plants at initialisation was 1 month. Then, we simulated a regular planting pattern with asynchronous banana plant stages (4; Fig. 2), i.e with different stages of plants in the same plot at the same time. In pattern 4, plant stages were randomly set from 1 month (planting) to 9 months (harvest); this situation is representative of old banana plots, which are unsynchronised because of the common practice of repeated sucker selection (Tixier et al., 2004; Lassoudière, 2007). For all patterns, 81 banana plants were distributed over a grid of 27 × 27 cells with a cell size of 0.8 m × 0.8 m, yielding a planting density of 1750 plants/ha.

At initialisation, different populations of adults of random age were equally distributed over the first column of the grid, representing the beginning of a rapid invasion due to putting an infested plot in fallow near the tested grid. For each pattern, we computed the time necessary for at least one adult to reach the column on the opposite side of the grid, the time-series of the mean intensity of attacks of each plant (*AC*), and the time-series of the percentage of plants with severe attacks (more than 20 cm of *AC*) over the entire period of simulation (600 days). Boundaries of grid were closed. Top and bottom edges represented a barrier; left edge the source of contamination that is unidirectional. As simulation stopped when one adult reached the last column of the grid, effect of right edge is absent. This experimental design allowed low edge effects, based on an infestation from one side to the other.

3.3. Sensitivity analyses

In a first step, we used the Morris method (Morris, 1991; Cariboni et al., 2007; see Appendix A) to discriminate the model parameters having the highest influence on the variability of mean and standard deviation of attacks, on four plots with different level of attacks (plots 8, 9, 10 and 16). Two ranges of parameter values were defined for this analysis, the first one corresponding to the uncertainty of estimates according to the literature, the other equally proportioned from −20 to 20% of the value in Table 1. Parameters equally discriminated using the two ranges were considered as the most influential.

In a second step, the parameters that were the most influential according to the first discrimination were tested one by one using a simple sensitivity analysis, the other parameter values being held constant. The model outputs were as before the variability of mean and standard deviation of attacks. For each parameter, different ranges of values were set, from 0 to 1 for biological rates and from 0 to an extreme value empirically defined (when model outputs no longer responded to parameter variations) for the other parameters. For each parameter value, 100 simulations were performed and the results arranged as boxplots showing the quartiles of the output distribution (Arrignon et al., 2007). For all the sensitivity analyses, plot 8 was chosen as representative of the studied plots, after examination of the first simulations (data not shown).

3.4. Statistical methods

For each plot used for model validation, smoothed distributions of the simulated attacks were plotted using 100 replicates of each simulation and compared with observations; this smoothing method is issued from Sheater and Jones (1991). Plotting smoothed distributions instead of histograms allow a better comparison between simulations and observations. The average distribution of the simulated attacks was compared to the observated attacks for each plot using the Kolmogorov–Smirnov (ks) test (Mellin et al., 2006). If the value of the probability associated to the ks test is greater than the level of significance (commonly 0.05), the null hypothesis of conformity (similar distributions) cannot be rejected. For each plot, the simulated mean and standard deviation of the distribution of attacks were compared to the observations over 100 replicates. The mean difference between observation and simulation was calculated using the root mean squared error (RMSE (Wallach and Goffinet, 1989)).

All statistical analyses were performed with the R software (R Development Core Team, 2008) using basic packages: “lattice” (for plotting the distributions of attacks using the kernel density estimate) and “sensitivity” (for sensitivity analysis using the Morris method).

4. Results

4.1. Model validation

Fig. 3 shows a good agreement between observed and simulated smoothed distributions of attacks for most plots. However, observed and simulated distributions were different for plots 2, 4, 6, 9, and 17 according to the Kolmogorov–Smirnov test ($P < 0.05$). For plots 2, 4, and 6, the model overestimated the frequency of high levels of attacks while it underestimated low levels of attacks (Fig. 4). For these plots, mean observed and simulated attack circumference (*AC*) were 10–15 and 25–30 cm, respectively. For plots 9 and 17, the model could not simulate the bimodal distribution of observed attacks. The model predicted well when the level of attacks at initialisation was relatively low (e.g. on plots 16 and 18, where the mean observed *AC* was 0 and 2 cm, respectively); and relatively high (plots 1, 11, 14, where the observed *AC* was 23–25 cm). The RMSE between the observed and simulated mean *AC* of the 18 plots was 7.7 cm; it improved when excluding plots 2, 4, and 6 (3.7 cm). The RMSE of the standard deviation was 2.6 cm for the 18 plots.

4.2. Sensitivity analysis

The Morris method showed that six parameters had a major influence on mean and standard deviation of the distribution of attacks: *DE*, *FH*, *ML*, *MRL*, *PE* (demographic parameters), and *G* (diameter of gallery; Appendix A, Table 1). Since the six parameters were similarly highlighted for the four tested plots, only the results for plot 8 were showed in Appendix A. *PE*, *MRL*, *G* and *FH* had a greater influence than *DE* and *ML*. On an extended range of variation, the increase in *PE* and *MRL* linearly decreased the mean level of attacks. The influence of *FH* (female fecundity) on the standard deviation of attacks decreased for more than eight eggs per week. For increasing values of *FH*, *DE*, *G*, and *ML*, the mean values of attacks increased linearly and then plateaued (Fig. 5).

4.3. Simulated effect of spatial arrangements of banana plants

The time necessary to cross the field was considerably higher for pattern 3 than for the other patterns, while a shorter time was found for pattern 4 (Table 2). This result remained the same when

Table 2
Time to cross the plot and mean level of attacks at 300 and 500 time steps for the four spatial arrangements of banana plants illustrated in Fig. 2 (initial population: 50 adults).

	Time to cross the plot (in days) ± SE	Mean *AC* at 300 days (in cm) ± SE	Mean AC at 500 days (in cm) ± SE
Pattern 1	184 ± 8	2.44 ± 0.08	6.89 ± 0.3
Pattern 2	197 ± 8	2.41 ± 0.09	7.03 ± 0.2
Pattern 3	395 ± 14	2.55 ± 0.08	7.47 ± 0.3
Pattern 4	170 ± 7	6.22 ± 0.16	16.24 ± 0.46

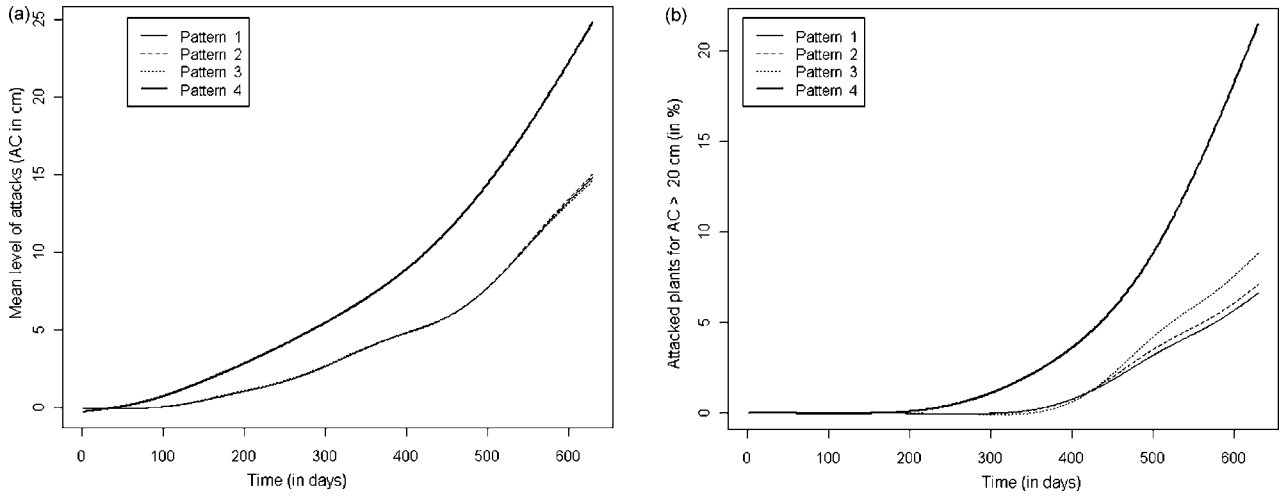

Fig. 6. Evolution of the mean intensity of attacks (a) and percentage of severe attacks (AC greater than 20 cm) (b), resulting from *C. sordidus* infestation of a plot. Initialization of the model was done for 50 individuals at one side of the plot, figuring a massive infestation from a neighboring field.

the initial population varied; times were reduced by half when the population varied from 50 to 400 individuals (data not shown). Mean levels of attacks at 300 days (harvest of first cycle) and 500 days (harvest of second cycle) were similar for planting patterns 1, 2 and 3 and twice as high for pattern 4.

Fig. 6 shows that the mean level of attacks increased to a higher level for pattern 4 than for patterns 1, 2, and 3. For patterns 1, 2, and 3, we observed a small inflexion of the mean level of attacks between 300–350 days and 500–550 days after planting (Fig. 6a). The percentage of plants with severe attacks (*AC* > 20 cm) increased faster for planting pattern 4, followed by patterns 3, 2, and 1 (Fig. 6b).

5. Discussion and conclusion

The individual-based COSMOS model accurately predicted the distributions of attacks of *C. sordidus* on banana plants for 13 out of 18 plots. This quality of prediction is attested for a large range of initial levels of attacks. The RMSE value of mean attacked circumference (7.7 cm) may be the consequence of overestimation of three validation plots and/or measurement error in the field. Furthermore, in the tested range of attacks, the standard deviation of the attacks in the plot was well maintained. Measurement error in the field could be due to an overlapping of some galleries in the same plant or to the presence of some galleries above or below the observation area. For three validation plots out of 18, the model overestimated the mean level of attacks. This overestimation could be explained by a greater predation of eggs in these plots than is accounted for by the model, predation of eggs being a major parameter according to the results of the sensitivity analyses. A highly variable density of *Pheidole* spp., a possible predator of *C. sordidus* eggs, was found among sites in a field trial in Uganda, ranging from 3.1 to 38.4 individuals per trap (Abera-Kalibata et al., 2008). Based on a recent survey in French West Indies, it seems that several species of ants are present in banana fields, including *Pheidole* spp. (Duyck, P.-F., pers. com.).

COSMOS compiles almost all of the existing knowledge about the biology of *C. sordidus*, benefiting from many experimental studies (Gold et al., 2001 and references therein). Nevertheless, our sensitivity analyses highlight the importance of better specifying key biological parameters to improve predictions, such as egg predation, adult mortality, and density-dependent effects. The level of egg predation is a key factor but is variable (Abera-Kalibata et al., 2008), which calls for further investigations. As explained by Carey (2001), little is known about mortality and longevity of insects, whereas they are fundamental epidemiological processes. The effect of density dependency of egg laying is also an influential parameter (Cuillé, 1950; Koppenhofer, 1993; Abera-Kalibata et al., 1999), but further studies should explore the whole range in which density dependency is established. It is also important to fill the lack of available data on predation rate of adults in the field, following the example of Sutherst et al. (2000) on ticks. For that purpose, field and laboratory experiments are currently conducted in French West Indies to identify the main predators of *C. sordidus*, and quantify their predation rates (Duyck, P.-F., pers. com.).

Our simulations on the effect of different spatial arrangements of banana plants on the epidemiology of *C. sordidus* show that planting in patches with a large distance between patches should limit the time necessary for the pest to colonise a new field. Indeed, in this case, only a small proportion of individuals is able to invade new patches. In contrast, the simulations indicate that the severity of attacks may increase when banana plants are planted in patches. Potting et al. (2005) in a modeling study on herbivores, found the same result, with a higher level of damages in patches than in rows. The pattern 3 figures patches with high concentration of plants. The hypothesis of resource concentration has been studied by Levine and Wetzler (1996). They have tested with an individual-based model the effect of planting decisions on attack frequencies by herbivorous insect pests, and they concluded that probability of host plant attack emerged partly as function of density of plants within patches. Furthermore, they estimate that probability of attack is function of radial distance

detection of host by insect. In COSMOS, radial detection is defined by weak dispersal abilities of adults, as defined by literature. These weak abilities contribute also to increase intensity of attacks inside patches. Planting banana regularly or in double rows resulted in similar simulated colonisation time and intensity of attacks. This is probably because in the case of double row spacing, the slow spreading of *C. sordidus* in large interstices between rows was compensated by fast spreading in small interstices inside rows. Unsynchronised banana plantation decreased the time of colonization of the plot by *C. sordidus* and increased the severity of attacks. In this pattern, at every time step, *C. sordidus* can find stages of banana plant suitable for egg laying. In contrast for the other patterns, the inflexion of mean *AC* observed at $t = 300–350$ days and $t = 500–550$ days may be explained by the lack of stages of banana plant suitable for egg laying after harvest. For management purposes at the landscape scale, farmers should avoid transforming a heavily infested field into fallow close to an unsynchronised field free of *C. sordidus*. At the field scale, planting in patches would limit the time of colonisation but after two or three cropping cycles, attacks might be severe. Such a strategy might be suitable for cropping systems with a limited number of cropping cycles. For cropping systems with more cropping cycles, regular and double row planting patterns of plantation would be more suitable.

The choice of the model type is governed by both spatial characteristics of habitat and insect traits. In a spatial insect model figuring infestation of melon by aphids, Lopes et al. (Lopes et al., 2009) introduced space implicitly because they consider local movement as negligible. In that model, populations of aphids are described by partial differential equations, figuring the continuous development of populations. In our case, weak dispersal abilities of *C. sordidus* have required to introduce space explicitly. Populations of *C. sordidus* are described at individual level because of its discontinuous development and the presence of all stages with different behaviour at the same time. These results show that COSMOS is an interesting tool to design planting schemes for the control of banana weevil. IBM models have rarely been used for such purposes on pests. Generally, they have dealt with spatial heterogeneity as a means of controlling pests by simulating the incorporation of non-attractant crops in the field (Potting et al., 2005; Choi et al., 2006).

The basic principles of the epidemiology of *C. sordidus* were successfully integrated in the COSMOS model. Further steps in developing this model should consist of integrating more management practices able to influence the epidemiology of this pest and to contribute to Integrated Pest Management (Huffaker and Gutierrez, 1999, p. 682), such as the use of resistant varieties, traps, and biological control agents, as suggested by Gold et al. (2001). This could be done by designing a sub-model that accounts for trapping. For this, existing algorithms (Byers, 1993; Branco et al., 2006) may be adapted to COSMOS. Furthermore, to design IPM schemes at the farm scale, the next step will be to upscale the model to a group of fields and to account for interfaces between fields.

The COSMOS model, by capturing the population trend of a tropical pest, is a powerful tool to analyse population processes of this pest in various management conditions. COSMOS can be seen as a 'virtual laboratory' (Charnell, 2008) for studying different agricultural practices that can influence the epidemiology of a pest. Emergence of population spatial properties from individual biology is the main driver of our study, as we consider that these practices will influence the individual behaviour of pests. In that way, IBMs can be applied to several pests, for which the spatial heterogeneity of agricultural practices influences biological parameters of individuals.

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Appendix A.

Twenty biological parameters of the insect (k "factors", according to the Morris method) were tested, considering their possible influence on the variability of mean and standard deviation of attacks. Each tested range was divided into four levels, corresponding to the resolution (Δ) at which the factor was examined. Following the method, for each factor, one of the four possible levels was randomly chosen, leading to a first sample. A first sensitivity run was done on this sample that consisted of 100 replicates of a one cropping cycle (200 time steps) simulation (see Section 3.2); the results were further averaged over the 100 replicates. Starting from the first factor sample, similar sensitivity runs were performed by considering successively each factor and increasing (or decreasing) its value by the quantity Δ. The combination of these $(k+1)$ sensitivity runs is called a trajectory and has to be repeated r times, thus leading to $r(k+1)$ sensitivity runs.

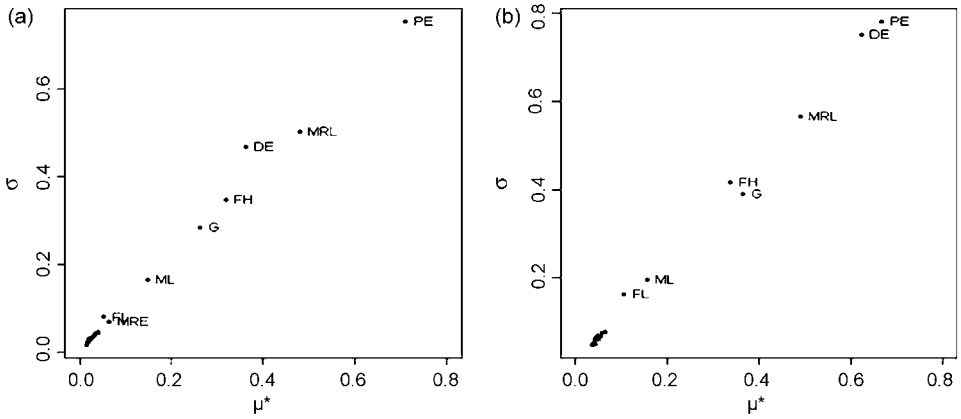

Fig. A.1. Sensitivity analysis on mean (a) and standard deviation (b) of attacks of *C. sordidus*. For each parameter, the tested range was defined according to the uncertainty of estimates according to published experimental studies.

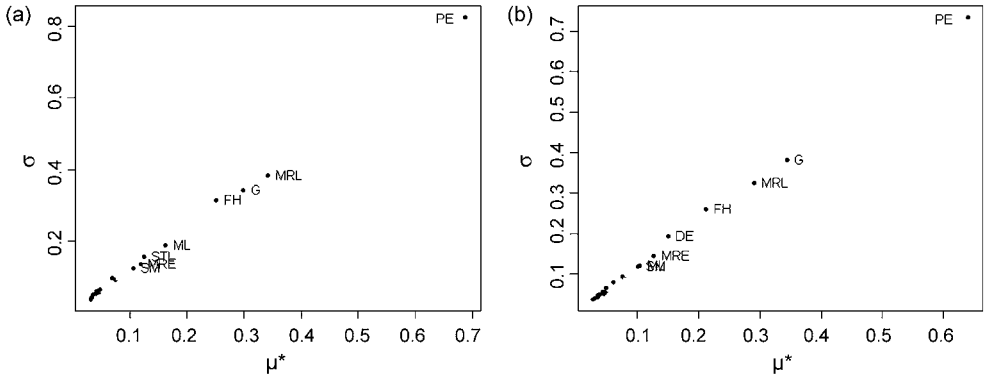

Fig. A.2. Sensitivity analysis on mean (a) and standard deviation (b) of attacks of *C. sordidus*. For each parameter, the tested range was equally proportioned (−20, −10, 10, 20% of the value in Table 1).

The elementary effect (EE_i) of a parameter θ on a trajectory j was calculated as:

$$EE_{i,j}(\theta) = \frac{y_j(\theta + e_i\Delta) - y_j(\theta)}{\Delta} \quad \text{(A.1)}$$

with $e_i = \pm 1$ and y_j the model output, here the mean or variance of attacks in the plot.

Thus, we generated a design experiment of 20 levels of parameters on 30 trajectories, which corresponded to a series of 630 sensitivity runs. The mean μ and the standard deviation σ of the absolute values of the elementary effects over the trajectories were used as sensitivity measures to ascertain the importance of the factors. A large μ indicates a large overall influence of the parameter and a large σ implies a dependency of the parameter on the value of the other parameters through non-linear or interaction effects (Figs. A.1 and A.2).

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Host range as an axis of niche partitioning in the plant-feeding nematode community of banana agroecosystems

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ABSTRACT

The stability and positive functions (such as pest regulation) of intensively managed agroecosystems can be enhanced by increasing biodiversity (in particular, by introducing cover plants or associated crops). Therefore, understanding modes of interspecific interactions among the phytophagous species, such as coexistence via host-plant partitioning, may allow manipulation of the balance between pest and non-pest species.

In the present study, we tested the hypothesis that a community of six plant-feeding nematode species in banana agroecosystems is structured by host plants. This was done using extensive data on the abundance of the different nematodes species on banana and associated weeds in Martinique. Because the purpose of this study was to focus on host-plant range, we eliminated the effects of temperature, rainfall, and soil type using a partial canonical correspondence analysis.

Host plants in banana agroecosystems have a marked influence on the plant-feeding nematode community structure. Host plants allow niche partitioning between some but not all pairs of species. The most evident pattern is the niche partitioning among the three nematodes considered long established in Martinique.

For pairs of species showing no host-plant niche partitioning, additional information regarding the colonisation and population dynamics over time both at the root and agroecosystem scale would allow better understanding of the equilibrium among species of the plant-feeding nematode community.

For management purposes, the modification of abundance of some host plants, which could be used as cover plants in the field, could change the balance among nematode species.

1. Introduction

The factors structuring phytophagous pest communities must be considered for agroecosystem management. In particular, understanding modes of interspecific interactions among the phytophagous species may allow managers to manipulate the balance between pest and non-pest species. Therefore, it is important to understand how phytophagous pest species coexist in agroecosystems. Species coexistence may be maintained by disturbance and predation and the interaction between these two factors (Gallet et al., 2007), spatial heterogeneity (Tilman, 1994), and niche partitioning (Giller, 1996; Chesson, 2000).

One way to enhance the stability and positive functions (such as pest regulation) of intensively managed agroecosystems is to increase biodiversity, in particular by introducing cover plants or associated crops (Tilman et al., 2002; Tylianakis et al., 2008). The idea is that the complexity of communities and food webs buffers against perturbations and therefore stabilizes the system (de Ruiter et al., 2005).

While monoculture of dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export involves intensive management, projects for re-introducing biodiversity by the way of plant cover, associated crops, and cultivated fallows have been initiated as parts of integrated pest management. Banana fields represent very simplified agroecosystems that are interesting to

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study in part because of the limited number of species in the associated plant community. Moreover, for applied purposes in agro-ecology, knowledge about the relationships among phytophagous species and between phytophagous and their host plants could allow manipulation of the structure of the phytophagous community by the choice of host plant. For example, the planting of cover crops during noncrop periods could modify the phytophagous community. Until now, the diversity of plants associated with the monoculture of dessert banana is limited to weeds. Because plant-feeding nematodes are the most damaging pests in these agroecosystems (Jones, 2000; Gowen et al., 2005), understanding the link between host-plant diversity and the structure of the community of plant-feeding nematodes is important.

Niche partitioning, i.e., the process driving competing species into different patterns of resource use or different niches, may occur through several different modes and on multiple temporal and spatial scales. First, nematode community composition is affected by different environmental factors (Bongers and Ferris, 1999; Ferris and Matute, 2003). At a regional scale, the ecological niches of plant-feeding nematodes may be partitioned by abiotic parameters in the agroecosystems such as climate or soil (Norton, 1989; Cadet et al., 2003; De Waele and Elsen, 2007). At the root scale, feeding on roots at different times of plant development or in different locations may also represent niche partitioning (Yeates, 1987). In this study, we focussed on the host-plant range component of the ecological niche (Yeates, 1999; Brinkman et al., 2008) by determining how six species of plant-feeding nematodes are affected by crop and associated weeds in banana agroecosystems.

Worldwide, bananas are attacked by many species of plant-feeding nematodes but only a few cause economically important damage. In Martinique, the nematode community parasitizing bananas is composed of the migratory endoparasites, *Radopholus similis* (Cobb, 1893) Thorne, 1949, and *Pratylenchus coffeae* Goodey, 1951; the endoparasites *Helicotylenchus multicinctus* (Cobb, 1893) Sher, 1961, and *Hoplolaimus seinhorsti* Luc, 1958; and the sedentary endoparasites *Meloidogyne* spp. and *Rotylenchulus reniformis* Linford & Oliviera, 1940. While all these species exploit the same resource (plant roots) and are able to parasitize a wide variety of host plants (Luc et al., 2005), they differ in life-history (sedentary versus migratory species) and reproductive strategy (parthogenetic versus amphimictic species).

Differences in when and how these species were introduced to Martinique Island and their associations with other crops are also important for understanding differences in nematode/host plant relationships. The burrowing nematode *R. similis* and the spiral nematode *H. multicinctus* are very closely associated with the development of banana crops and have thus arguably been introduced very recently, probably with the first introduced banana plant materials in the Caribbean early in the 16th century (Marin et al., 1998). *R. similis* is native to the Southeast Pacific rim and is the only species within the genus *Radopholus* to be detected outside its centre of origin. Marin et al. (1998) and more recently Price (2006) show how the dispersal of *R. similis* was definitely linked to the dissemination of bananas. The reniform nematode *R. reniformis* is a pan-tropical species associated with many different hosts. Because of its ability to enter into anhydrobiosis (Womersley and Ching, 1989), it can easily be spread by winds and is therefore considered indigenous in the West Indies. The other nematode species (*H. seinhorsti*, *Meloidogyne* spp., and *P. coffeae*) are also widespread as pan-tropical species and are associated with many horticultural crops (Luc et al., 2005). These three species were probably present in the West Indies long before the introduction of bananas.

Beyond banana, these six nematode species are able to exploit a number of weeds present in banana agroecosystems (weed species and families in Martinique are listed in Table 1). While *R. similis* and *H. multicinctus* are closely associated with these banana agroecosystems, the four other nematode species are mostly found in other ecosystems including natural habitats (Luc et al., 2005).

The purpose of this study is to analyse whether and how plant-feeding nematodes partition host plants in banana agroecosystems. While abiotic factors including climate and soil may profoundly affect nematode community structure (Norton, 1989; Cadet et al., 2003), they are not the objects of the present study. The detailed study of the influence of these abiotic factors in Martinique would require the collection of many samples one unique host plant (banana) in different parts of the island. However, climate and soil type were included in our analyses to control for their effects.

In this study, we tested the hypothesis that the plant-feeding nematode community is structured by host plants. We did this by collecting weeds in banana fields and by determining the abundance of each nematodes species on the different host-plant species to answer the following questions: (i) Do the nematodes species have different host ranges? (ii) Is the nematode community structure affected by host-plant weeds associated with bananas? (iii) Is there a host-plant niche partitioning that could promote coexistence among the different species? (iv) Is host-plant niche partitioning related to the introduced versus indigenous status of the plant-feeding nematode species?

2. Materials and methods

2.1. Field data

All samples were collected in Martinique (French West Indies, 14°N, 61°W). Field surveys were regularly conducted between 2002 and 2008. The whole island was prospected year round for associated weeds in banana crops. We used published data on the presence of the nematode species on the different host plants (Quénéhervé et al., 2006) and supplemented them with new data collected with the same method.

We collected 556 weed samples from fields in the different parts of the island. Each sample included the shoots and roots of each plant. After identification of the plant to species (Fournet, 1978; Fournet and Hammerton, 1991), all root samples were carefully washed under tap water to remove soil particles and fine entangled roots. The nematodes were extracted from a 20-g fresh root subsample per plant (carefully picked out under a magnifier) in a mist chamber (Seinhorst, 1950). For 2 weeks, a fine mist of water was sprayed continuously over the roots. Active nematodes emerged and were recovered from the water that collects below. Extracted nematodes were counted twice: after 1 week and again after 2 weeks in the mist chamber using a counting dish and a stereomicroscope. Dry weights of roots were obtained by placing roots at 60 °C in a drying oven. The entire database comprises 247,332 nematodes.

Mean annual temperature and cumulative annual rainfall in the different locations on Martinique were provided for a 30-year period by Météo-France Martinique, Service Climatique. Soil type (Andosol, Ultisol, Vertisol) was determined using Colmet-Daage and Lagache (1965) soil type map.

2.2. Statistical analyses

We used canonical correspondence analysis (CCA) with four factors: temperature, rainfall, soil type, and plant species. This method was introduced by ter Braak (1986). It has been developed to study the relationship between species composition and environment within sites. Here the basic sampling unit is a weed sample separated in space or time from other samples. CCA is an

Table 1
Recorded host plants and relative abundance of six species of plant-feeding nematodes in banana agroecosystems from Martinique. Stars indicate introduced plant species in Martinique (according to Fournet (1978)).

Family	Species	Number of samples	Number of nematodes	Number/g dw[a]	Species relative abundance					
					Meloidogyne spp.	*Helicotylenchus multicinctus*	*Radopholus similis*	*Pratylenchus coffeae*	*Rotylenchulus reniformis*	*Hoplolaimus seinhorsti*
Amaranthaceae	1 *Amaranthus dubius*	19	9206	973	0.40	0.43	0.04	0.01	0.12	
	2 *Amaranthus spinosus*	5	1652	2361		1.00				
Araceae	3 * *Caladium bicolor*	5	6224	5460			1.00			
	4 * *Colocasia esculenta*	15	13661	3614	0.92			0.06	0.02	
	5 *Dieffenbachia seguine*	5	410	109	0.66				0.32	0.02
	6 *Xanthosoma violaceum*	10	24621	11191	0.79	0.01			0.20	
Asteraceae	7 * *Emilia fosbergii*	5	42	28					1.00	
	8 *Mikamia micrantha*	16	3779	496	0.01				0.99	
	9 *Vernonia cinerea*	5	12	12	1.00					
Capparidaceae	10 *Cleome aculeate*	11	120	42	0.36			0.01	0.39	0.24
	11 * *Cleome rutidosperma*	11	611	25	0.38	0.10	0.11		0.33	0.08
Commelinaceae	12 *Commelina diffusa*	15	25618	14723			0.13		0.84	0.03
Convolvulaceae	13 * *Ipomoea eriocarpa*	1	16	6					1.00	
	14 *Ipomoea tiliacea*	3	0	0						
Cucurbitaceae	15 * *Momordica charantia*	1	8561	4920	0.99	0.01				
Cyperaceae	16 * *Cyperus esculentus*	19	1105	111	0.96	0.04				
Euphorbiaceae	17 *Euphorbia cyathophora*	8	93	42			0.50		0.49	0.01
	18 * *Euphorbia heterophylla*	21	395	120	0.05	0.72	0.11		0.12	
	19 *Phyllanthus amarus*	20	1003	141	0.03	0.93	0.02		0.02	
Fabaceae	20 *Centrosoma pubescens*	1	0	0						
Malvaceae	21 *Sida acuta*	5	0	0						
	22 *Urena lobata*	8	131	21	0.83	0.05		0.12		
Melastomataceae	23 *Clidemia hirta*	11	687	22	0.49		0.51			
Mimosaceae	24 *Mimosa pudica*	12	2366	219	0.60			0.01	0.04	0.35
Moraceae	25 *Cecropia schreberiana*	8	1412	200	0.01	0.19	0.01		0.79	
Musaceae	26 * *Musa AAA Cavendish*	36	68007	1022	0.29	0.40	0.27		0.03	0.01
Myrtaceae	27 * *Psidium guajava*	1	20	8	0.75	0.25				
Onagraceae	28 * *Ludwigia abyssinica*	1	3	1			1.00			
Oxalidaceae	29 *Oxalis barrelieri*	1	6	75		0.67			0.33	
Passifloraceae	30 *Passiflora edulis*	3	169	220	0.03				0.94	0.03
Piperaceae	31 *Peperomia pellucida*	11	3080	1721	0.99		0.01			
Poaceae	32 *Digitaria horizontalis*	15	122	16		1.00				
	33 *Echinochloa colona*	26	4482	648	0.12	0.16	0.45			0.27
	34 *Eleusine indica*	38	16854	612	0.69	0.25	0.06			
	35 *Eragrostis pilosa*	1	181	133			0.03			0.97
	36 *Leptochloa filiformis*	14	282	47	0.83		0.04	0.06	0.07	
	37 * *Panicum maximum*	1	7	5			1.00			
	38 *Paspalum fasciculatum*	15	1052	100	0.23	0.03	0.48	0.20	0.06	
	39 * *Rottboellia cochinchinensis*	10	138	37		0.28	0.25	0.29	0.18	
	40 * *Setaria barbata*	15	176	125	0.24	0.39	0.25	0.04	0.08	
	41 * *Sorghum halepense*	7	129	5	0.34	0.20				0.46
Rubiaceae	42 *Spermacoce verticillata*	6	0	0						
Solanaceae	43 *Physalis angulata*	7	191	185		0.85	0.12	0.03		
Solanaceae	44 *Solanum americanum*	30	12522	510	0.70	0.06	0.06		0.18	
	45 *Solanum torvum*	20	3068	180	0.02	0.17	0.23		0.58	
Urticaceae	46 *Laportea aestuans*	10	467	218	0.80	0.11			0.09	
	47 * *Phenax sonneratii*	40	34508	1610	0.10	0.10	0.15		0.65	
	48 *Pilea microphylla*	1	144	360	0.97					0.03

[a] Number of nematodes/g dw of root.

extension of correspondence analysis (CA) in which samples are given linear weights so as to maximise the variance among species. CCA looks for coefficients of environmental variables to obtain a site score that maximises the variance of the average positions of species. We completed this analysis by a partial CCA (ter Braak, 1988) to eliminate the effects of temperature, rainfall, and soil type. All computations and graphical displays were carried out using R software, with routines available in the vegan package and the ADE4 package (Chessel et al., 2004).

We then analysed the effects of host-plant species, plant class (monocotyledons or dicotyledons), and plant introduction status (indigenous or introduced) on the abundance of each nematode species using a generalised linear model (GLM) with Poisson error. Plant introduction status is given in Table 1. For each nematode species, a reference model, including all significant terms of environment (temperature, rainfall, and/or soil type) and interactions, was used for comparing the effect of plant species, plant class, and plant introduction status. Overdispersion was accounted for using Quasi-Poisson in place of Poisson models in R (Crawley, 2007).

3. Results

From field surveys, 48 different plant species hosting the six plant-feeding nematodes species were collected (Table 1). Among these, at least 16 plant species are considered as recently introduced in Martinique (Fournet, 1978; Fournet and Hammerton, 1991).

CCA with all factors shows the influences of temperature, rainfall, and soil type on the relative abundance of nematodes species (Fig. 1a, proportion of variance of axis 1: 0.34, axis 2: 0.24, axis 3: 0.16, axis 4: 0.15, axis 5: 0.11). In the same analysis, some host-plant species were placed along a climate and soil type axis, indicating

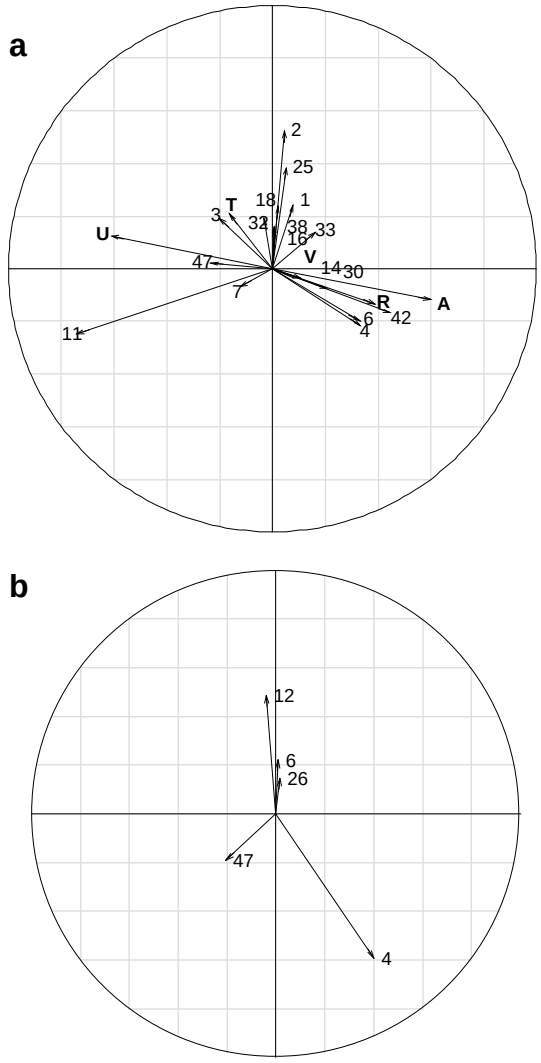

Fig. 1. Canonical correspondence analysis of the relationship between plant-feeding nematodes species and host-plant species. The two plots display correlations >0.1 between variables and the first two axes of the CCA for the first plot (a) and the partial CCA removing the effects of temperature, rainfall, and soil type for the second plot (b). Numbers correspond to the host-plant species presented in Table 1. T: Temperature, R: Rainfall, A: Andosol, U: Ultisol, V: Vertisol.

that these host plants were not randomly distributed regarding climatic and soil conditions. The partial CCA (Fig. 1b, proportion of variance of axis 1: 0.99, axis 2: 0.01) allows controlling for the effect of temperature, rainfall, and soil type. Independent to these environmental variables, five host plants were strongly correlated to changes in abundance of the different nematodes species; these host plants were *Musa* spp. (banana) and four weeds, *Commelina diffusa*, *Colocasia esculenta*, *Phenax sonnerati*, and *Xanthosoma nigrium* (Fig. 1b). The nematodes *Meloidogyne* spp., *H. multicinctus*, and *R. similis* had a large distribution (as indicated by the large ellipse in Fig. 2). The centroids for *Meloidogyne* spp. and *H. multicinctus* were particularly close together. In contrast, the three other species, *P. coffeae*, *R. reniformis*, and *H. seinhorsti* had smaller distributions (as indicated by smaller ellipses in Fig. 2). The centroids of ellipses of these three last species are clearly separated, and the ellipses containing 90% of individuals according to the binormal distribution of points indicate a very weak overlap (Fig. 2).

The frequency distribution of the relative abundance of the six nematode species shows that *H. seinhorsti* and *P. coffeae* have a high relative abundance on a few plant species: about 80% of the relative abundance of each of these two nematode species derives from only four host plants (*Eragrostis pilosa*, *Sorghum halepense*, *Mimosa pudica*, and *Echinochloa colona* for *H. seinhorsti* and *Rottboellia cochinchinensis*, *Paspalum fasciculatum*, *Urena lobata*, and *C. esculenta* for *P. coffeae*) (Fig. 3). Distribution of the relative abundance is smoother for the four other species, with a maximum relative abundance between 7 and 10% for one host plant. The frequency distributions of relative abundance show that host ranges of *H. seinhorsti*, *R. reniformis*, and *P. coffeae* are mostly separated while the ones of *Meloidogyne* spp, *H. multicinctus*, and *R. similis* overlap.

Results of the GLM analysis are presented in Table 2. Once the significant terms of environment (temperature, rainfall, soil type, and interactions) are accounted for in a reference model, the addition of the 'plant species effect' is significant for all these nematode species. Effect of plant class (monocotyledon or dicotyledon) is significant for *P. coffeae* and *R. reniformis*, these species being more abundant on dicotyledons than on monocotyledons. Effect of plant introduction status is significant for *R. similis*, *P. coffeae*, and *H. seinhorsti*. *R. similis* and *P. coffeae* are more abundant on introduced plant species while *H. seinhorsti* is more abundant on indigenous plant species.

4. Discussion

4.1. Host-plant range and nematode community structure

Host plants in banana agroecosystems have a marked influence on the community structure of plant-feeding nematodes. Results of the CCA and GLM show that host plant greatly affects the abundance of each of the six plant-feeding nematode species. All six nematode species have a wide range of hosts, including from 9 to 30 plant species belonging to numerous families. The six nematode species can thus be considered as polyphagous. Although the host ranges of these species overlap, the relative abundance of each nematode species differs among different host plants, indicating different preferences in host exploitation.

Meloidogyne spp., *H. multicinctus*, and *R. similis* are present on most plants collected. These species are generally considered very polyphagous (Luc et al., 2005). The genus *Meloidogyne* on *Musa* mainly comprises two species, *Meloidogyne arenaria* and *Meloidogyne incognita* (Cofcewicz et al., 2005), which were not differentiated in our study. Species belonging to the *Meloidogyne* genus are generally determined by electrophoresis, and this method could not be used in a wide field survey like the one in our study.

While the six nematode species are polyphagous, i.e., they are able to parasitize many host plants, frequency distribution of relative abundance shows that *P. coffeae*, *R. reniformis* and *H. seinhorsti* specialise on different host plants. In particular, *R. reniformis and P. coffeae* are more abundant on dicotyledons than monocotyledons. This preference of *R. reniformis* for dicotyledons was mentioned by Gaur and Perry (1991).

Although ectoparasitic nematodes also occur in the soil of banana agroecosystems, these species are usually in low densities and are less likely to be involved in competitive interactions (Luc et al., 2005). Collection of soil samples, in addition to root samples, would increase our understanding of interactions between endoparasitic and ectoparasitic nematodes.

4.2. Niche partitioning and coexistence via host plants

Host plants allow niche partitioning among some nematode species. The most evident example of this is the niche partitioning among *P. coffeae*, *R. reniformis*, and *H. seinhorsti*. Both the ellipses of the partial CCA and the frequency distributions of relative

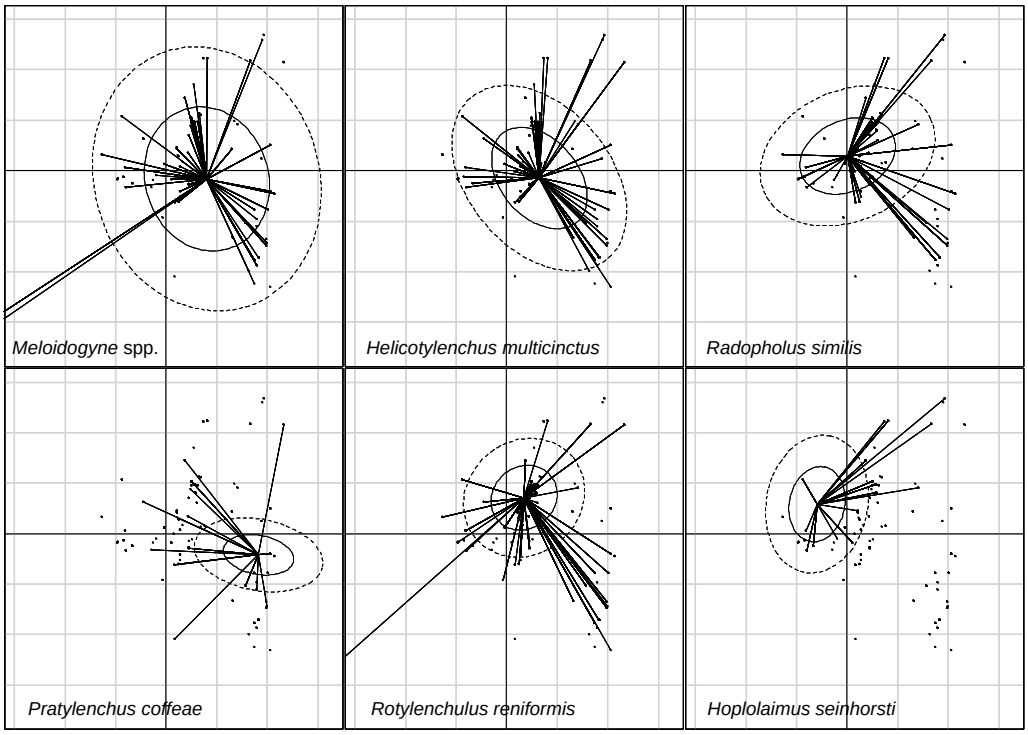

Fig. 2. Biplots of the normalized coordinates of the sites, constrained by the host-plant species, and the coordinates of the nematode species. In each plot, a grid indicates the scale; the length of the square side is 1. In each plot, the dots indicate the samples, the straight lines indicate the presence of nematode species in samples, and the ellipses surround the position of the nematode species providing an index of the dispersion around the species centroid (50% and 90% of individuals collected are expected to be in the ellipse formed by the continuous line and the broken line, respectively). These ellipses are representations of the diversity of the host-plant species used by the nematodes.

abundance show very weak overlap among these species in their exploitation of host plants. This pattern is even stronger between *H. seinhorsti* and *P. coffeae*. Also, ellipses of the partial CCA indicate relatively low overlap between *R. similis* and *P. coffeae*. Overlap is strong between all other pairs and especially with *Meloidogyne* spp. and *H. multicinctus*, whose dispersion ellipses overlap those of all other species.

Interspecific competition in the field has been strongly suggested between *Meloidogyne* spp. and *R. similis*, *Meloidogyne* spp. and *P. coffeae*, and *H. multicinctus* and *R. similis* (Quénéhervé, 1990; Moens

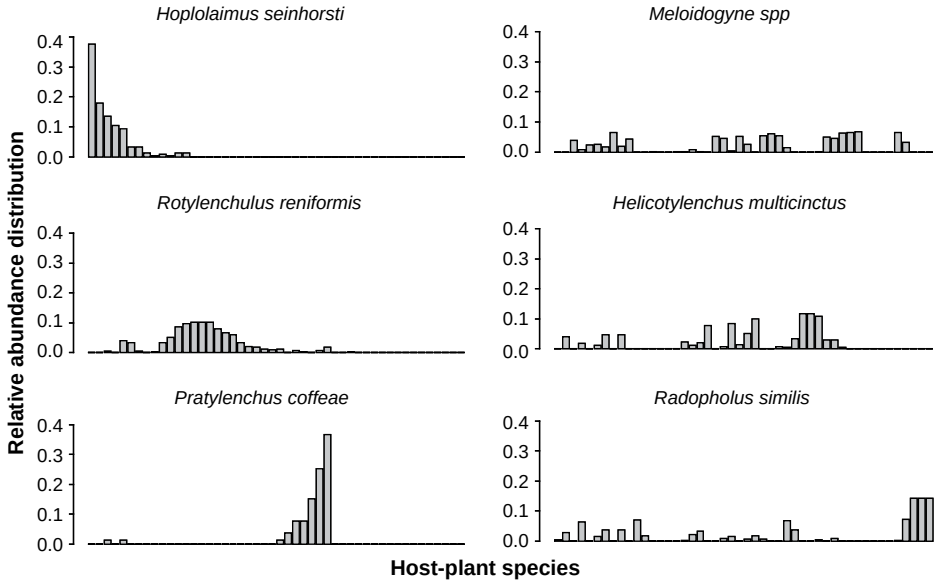

Fig. 3. Frequency distribution of the relative abundance on the 48 host plants for each plant-feeding nematode species. Because *Hoplolaimus seinhorsti*, *Rotylenchulus reniformis*, and *Pratylenchus coffeae* show a strong host-plant partitioning, host-plant species are ordered to illustrate the niche separation between these species. Frequency distributions of *Meloidogyne* spp., *Helicotylenchus multicinctus*, and *Radopholus similis* are given for the same order of host-plant species. It is not possible to order host plants showing niche separation with these three last nematode species. Number of plant species from left to right: 35, 41, 24, 33, 10, 11, 40, 48, 26, 5, 18, 12, 30, 7, 13, 8, 25, 47, 45, 29, 6, 44, 18, 46, 1, 43, 36, 4, 22, 38, 39, 2, 32, 19, 27, 34, 16, 15, 9, 14, 20, 21, 42, 31, 23, 3, 28, 37. Correspondence between number and host-plant names is given in Table 1.

Table 2
Results of the analysis of deviance for abundance of each nematode species. Effects of host-plant species, host-plant class (monocotyledon or dicotyledon), and host-plant introduction status are compared with a reference model for each nematode species; also included are all the significant terms of environment (mean annual temperature = t; mean annual rainfall = r; soil type = s; and interactions). Δ*Dev* corresponds to change in deviance due to the addition of the effect term to reference model. Significant effects are indicated in bold. Introduction status is given in Table 1.

Nematode species	Reference model			Plant species			Plant class			Plant introduction status		
	Terms	residual *d.f*	residual *Dev*	Δ*Dev*	Δ*d.f*	*P*	Δ*Dev*	Δ*d.f*	*P*	Δ*Dev*	Δ*d.f*	*P*
Meloidogyne spp.	1	554	1,648,420	769,865	47	**<0.0001**	48,098	1	0.216	410	1	1
Helicotylenchus multicinctus	1 + t + s + t:s	550	330441	138,003	47	**<0.0001**	1648	1	1	702	1	1
Radopholus similis	1 + t + r + s + t:p + r:s	548	312,411	138,358	47	**<0.0001**	3853	1	0.198	37127	1	**0.0002**
Pratylenchus coffeae	1 + t + r + s + t:s + t:r	548	152,58.7	9011.2	47	**<0.0001**	2233.8	1	**<0.0001**	1938.3	1	**<0.0001**
Rotylenchulus reniformis	1 + r	552	1,865,854	1,150,504	47	**<0.0001**	196,465	1	**0.001**	27544	1	0.284
Hoplolaimus seinhorsti	1 + t + r + s	550	43,100	25,460	47	**<0.0001**	58	1	1	8648	1	**<0.0001**

et al., 2006; Tixier et al., 2006; Quénéhervé, 2008; Tixier et al., 2008). Because exploitation competition for the same resource is likely to occur (and perhaps interference competition via degradation of this resource), coexistence by host-plant niche partitioning is therefore possible among *P. coffeae*, *R. reniformis*, and *H. seinhorsti*, and between *R. similis* and *P. coffeae*. Coexistence among other pairs of species is probably dependent on other mechanisms.

At the root system scale, another axis of the ecological niche is the distance from the rhizome (Quénéhervé, 1990). On banana roots, *R. similis* is more restricted to the closest part of the rhizome compared to other species (Quénéhervé and Cadet, 1985). This is especially evident when *R. similis* competes with *H. multicinctus* (Quénéhervé, 1990). *R. similis* is a migratory endoparasite, able to penetrate any type of root (primary, secondary, and tertiary) and at any position along the root (as is also true for *H. multicinctus* and *H. seinhorsti*) while *R. reniformis* and *Meloidogyne* spp. are sedentary endoparasites that penetrate only at the tip of secondary or tertiary roots just behind the growing meristem.

Coexistence may be insured by mechanisms other than niche partitioning. First, source-sink with migration from outside banana crops is possible; while *R. similis* and *H. multicinctus* seem very associated to banana crops (Gowen et al., 2005), the four other species are found in many other habitats and in particular in vegetables and tuber crops (Luc et al., 2005). Second, coexistence may be enhanced by predation; however, the sampling and extraction methods used in this study do not allow an assessment of predation or of apparent competition mediated through predation. Further studies that included collection of the free-living nematodes, including predacious and omnivorous nematodes, would increase our understanding of these putative species interactions. Third, the life histories of some of these species are still partially unknown, and they may have different colonisation strategies. While plant-feeding nematodes are difficult to rank in the classical *c-p* scale, they can be ranked as *r-K* strategists based on their growth rates (Bongers, 1990). Different colonization abilities and different responses to disturbance (fallow period) and/or spatial heterogeneity (asynchrony of banana trees) may allow coexistence by competition–colonisation trade-off (Tilman, 1994).

4.3. Coexistence and status of introduction of nematodes

Invasions by non-native species often have profound effects on ecosystem function and recipient community structure (Williamson, 1996; Juliano and Lounibos, 2005). However, there are many examples where biological invasions did not lead to the extinction of resident species, i.e., indigenous and invasive species may coexist (Sax et al., 2002; Bruno et al., 2005; Duyck et al., 2006).

Meloidogyne spp., *P. coffeae*, *R. reniformis*, and *H. seinhorsti* were probably already present (being indigenous or previously established) in Martinique when banana was introduced and *R. similis* and *H. multicinctus* colonised the island (see Introduction). Niche partitioning via host plant exists among three of the already established species (*P. coffeae*, *R. reniformis*, and *H. seinhorsti*), which is in accordance with the fact that these species have probably been in contact for a long time and have possibly co-evolved. *P. coffeae* occurs more frequently on introduced plant species, however the three nematode species are also found on many indigenous plants. *R. similis* and *H. multicinctus* cover the niche of all pre-existing species, and there is no host-plant niche partitioning except a moderate degree of partitioning between *R. similis* and *P. coffeae*. Thus, in contrast to the strong niche partitioning among already established species (except *Meloidogyne* spp., which have probably more different life-history traits, see above), there is low potential for niche partitioning between recent invaders (*R. similis* and *H. multicinctus*) and established species because most of the host-plant niches of the established species are included in those of the recent invaders.

4.4. Implications for banana agroecosystem management

Our results highlight that modifying the abundance of some host plants may change the balance among nematode species in banana agroecosystems. The burrowing nematode *R. similis* is the most damaging nematode in banana crops (Gowen et al., 2005). No niche partitioning between this species and other nematode species regarding host plant has been observed except with the lesion nematode *P. coffeae*, which is the second most damaging nematode (Quénéhervé, 2008). For example, *C. esculenta* will favour populations of *P. coffeae* and *Meloidogyne* spp. and disfavour populations of *R. similis*. In contrast, some weeds (e.g., *C. diffusa*) support high numbers of *R. similis* and may increase numbers of this species. From a practical point of view, these plant species should be removed during fallow.

H. seinhorsti and *R. reniformis* are considered less damaging nematodes on bananas (Gowen et al., 2005). Because there is host-plant niche partitioning with *P. coffeae*, plants favouring *H. seinhorsti* may prevent population growth of *P. coffeae*. *Eragrostis ilosa* could be a good candidate if additional data confirm that it does not support large numbers of *P. coffeae* or *R. similis*. However, *H. seinhorsti*, *R. reniformis*, and *Meloidogyne* spp. can also damage crops if present in large numbers. For example, high numbers of *Meloidogyne* spp. in the absence of *R. similis* induced severe damage on banana (Jones, 2000: pp. 307–314). An effective strategy for regulation of nematode pests could be to choose a set of associated host-plant species that favour a nematode species that is a weak pest of banana but a good competitor against serious nematode pests of banana on the associated host plant.

In conclusion, host-plant partitioning in banana agroecosystems is considerable among some plant-feeding nematode species, especially those considered long established in Martinique. However, other factors that could promote coexistence and

equilibrium among species should be explored. Additional information about colonisation and population dynamics over time both at the root and agroecosystem scale would increase our understanding of equilibrium among species of the plant-feeding nematode community.

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BIODIVERSITY RESEARCH

Can more *K*-selected species be better invaders? A case study of fruit flies in La Réunion

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ABSTRACT

Invasive species are often said to be *r*-selected. However, invaders must sometimes compete with related resident species. In this case invaders should present combinations of life-history traits that give them higher competitive ability than residents, even at the expense of lower colonization ability. We test this prediction by comparing life-history traits among four fruit fly species, one endemic and three successive invaders, in La Réunion Island. Recent invaders tend to produce fewer, but larger, juveniles, delay the onset but increase the duration of reproduction, survive longer, and senesce more slowly than earlier ones. These traits are associated with higher ranks in a competitive hierarchy established in a previous study. However, the endemic species, now nearly extinct in the island, is inferior to the other three with respect to both competition and colonization traits, violating the trade-off assumption. Our results overall suggest that the key traits for invasion in this system were those that favoured competition rather than colonization.

Keywords

Biological invasions, competitive displacement, life-history traits, *r–K* trade-off, Tephritidae.

INTRODUCTION

Biological invasions are now considered one of the most important components of human-induced recent changes in the biosphere (Vitousek *et al.*, 1996), and have dramatic impacts on both species distributions and global biodiversity (Lodge, 1993; Mack *et al.*, 2000; Mooney & Cleland, 2001). Thus, the identification of biological traits typical of potential invaders (Crawley, 1986; Gray, 1986; Mack, 1996; Kolar & Lodge, 2001) and of features of invasible habitats (Lonsdale, 1999; Levine, 2000; Stachowicz *et al.*, 2002; France & Duffy, 2006; Richardson & Pysek, 2006) has become an important challenge. Despite an increasing number of studies, it has been notoriously difficult to obtain robust generalizations, both because of the heterogeneity of taxa and ecosystems affected by invasion, and because of the predominant effect of variation in propagule pressure among case studies (Lonsdale, 1999; Kolar & Lodge, 2001). A pervasive historical paradigm, although with quite ambiguous empirical support (see, e.g. Mack, 1996; Kolar & Lodge, 2001), is the assumption that invasive species should be good colonists (Elton, 1958; Lodge, 1993; Williamson, 1996). Invasive species are defined on a biogeographical basis, as those that have recently been introduced and have established viable populations far from their original distribution areas (Williamson, 1996). In contrast, colonists have been historically defined by a set of biological traits including short generation times, short juvenile phase, high reproductive effort, production of many small, mobile offspring, and in some cases vegetative reproduction (Pianka, 1970). There has been much debate on the reality and exact nature of the 'colonist's syndrome' (MacArthur, 1962; Pianka, 1970; Grime, 1977; Stearns, 1992; Mueller, 1997; Reznick *et al.*, 2002). Because the intrinsic growth rate is positively affected by such traits, they were termed '*r*-selected traits' by Pianka (1970) and said to be advantageous in non-competitive environments such as early successional or otherwise unstable habitats (MacArthur, 1962). This theory is based on the assumption of a trade-off among traits so that competitive ability and *r* cannot be maximized at the same time (MacArthur, 1962; Tilman, 1994; Kneitel & Chase, 2004). Without questioning this principle, modern theory of life-history evolution has complexified this view, showing that a low sensitivity of early-life stages to competition, not necessarily the absence of competition, was the key condition for the evolution of the so-called '*r*-traits' (Charlesworth, 1994; Mueller, 1997; Reznick *et al.*, 2002). With this limitation in mind, the historical conception that invaders should be good colonists still must rely on two assumptions: (1) invaded habitats are often unsaturated or otherwise resemble the habitats that favour *r*-traits in native ranges, and (2) invasion is limited by the ability to rapidly spread and grow in numbers in such habitats. Both assumptions have received some empirical support, although not completely

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conclusive. Indeed, disturbed habitats seem more prone to invasions (Lozon & MacIsaac, 1997; see, however, Bruno *et al.*, 2004), and some comparisons between invaders and non-invasive related taxa highlight the role of traits typical of the so-called *r*-strategy (see Rejmanek, 1996 and references below). The best-known example is found in invasive conifers, in which several large-scale comparisons have revealed higher relative growth rate, smaller seed mass, shorter juvenile phase, and more frequent seed production in comparison to non-invasive species (Rejmanek & Richardson, 1996; Grotkopp *et al.*, 2002; Richardson & Rejmanek, 2004). Similarly, invasive populations of *Spartina alterniflora* show earlier and larger reproductive effort, higher investment into vegetative reproduction, and lower self-incompatibility than their congeners from the native range in common garden experiments (Davis, 2005). Note, however, that component traits, rather than the intrinsic rate of increase itself, have been used in such studies.

Apart from the need for more data, a more basic criticism of the *r*-strategy hypothesis is that different contexts are expected to favour different types of invaders, and no single combination of traits can be successful everywhere (Holdgate, 1986; Lodge, 1993; Mack *et al.*, 2000; Radford & Cousens, 2000; Facon *et al.*, 2004; Richardson & Pysek, 2006). Invasion depends on an interaction between a species' traits and characteristics of the recipient ecosystem (Byers, 2002; Thuiller *et al.*, 2006; see also the 'niche opportunity' concept in Shea & Chesson, 2002), especially the resident community (Shea & Chesson, 2002). A high intrinsic rate of increase by itself cannot impede invasion; however, if *r*-traits trade-off with traits important for the interaction with resident species, the relationship between invasive ability and *r* could be negative instead of positive. For example, the *r*-selected traits in the oyster *Crassostrea ariakensis* do not make it a good invader because they come with a low investment in defence and high susceptibility to predation by blue crabs (Bishop & Peterson, 2006).

Competition is an important component of the biotic environment of invasive species (Stachowicz & Tilman, 2005). Of course, examples of invaders with traits typical of colonists are often associated with either disturbed habitats (case of woody plants, Rejmanek, 1996) or previously empty habitats (mudflats invaded by *S. alterniflora* in the US Pacific coast; Davis, 2005). However, not all invasions happen in such contexts (Byers, 2002; Daehler, 2003; Evans, 2004). In contexts where competition occurs and is an important constraint on the demography of invasive species, one expects, based on trade-off theory (Kneitel & Chase, 2004), a negative relationship between *r* and invasive success. Such a context has recently been identified in a group of four species of polyphagous fruit flies (tephritids) now inhabiting the island of La Réunion (Duyck *et al.*, 2004a).

The family Tephritidae is well known for multiple invasions that pose important economic problems in fruit or vegetable crops in tropical and subtropical areas worldwide (Duyck *et al.*, 2004a). Historical records are available because of the economic importance of these species, and they are easy to rear under laboratory conditions. Four species of ecologically very similar tephritids now inhabit La Réunion, including an endemic species *Ceratitis catoirii* Guérin-Mèneville, and three others that have successively invaded: *Ceratitis capitata* (Wiedemann) in 1939, *Ceratitis rosa* Karsch in 1955, and *Bactrocera zonata* (Saunders) in 1991. Each newly arrived species has partially excluded and/or displaced each other, and has become largely dominant over previous ones, at least in the lowlands (< 100 m a.s.l.), where the four species now coexist. An exception to this pattern is that *C. rosa* continues to be dominant in the highlands because the climate there is unsuitable for the other species (Duyck *et al.*, 2006b). Duyck *et al.* (2006a), studying larval exploitative competition in fruits and interference between adult females for access to laying sites, concluded that competitive interactions were hierarchically organized, with recently arrived species systematically dominant on previous ones. In the same study, natural densities and co-infection rates in field-collected fruits were such that interspecific competition must occur in the field as it did in the laboratory.

This system is a good opportunity to test our hypothesis of a negative relationship between invasivity and *r*-traits, not only because competition has been a major component of invasions (Duyck *et al.*, 2006a), but also because the species are similar enough, phylogenetically and ecologically, to provide meaningful comparisons of life-history traits and document potential trade-offs. We here use experiments in a common laboratory environment to establish the life tables of all four species (including both the intrinsic rate of increase and its component traits) and to test whether successive invaders are characterized by decreasing *r* (or component traits), as predicted by our hypothesis. Our approach does not contrast invaders vs. non-invasive related species as done in previous studies of the relationship between traits and invasiveness; instead we compare invaders to their competitors (endemic and introduced) because our previous studies have shown that competition was a strong limit to invasion in this system (Duyck *et al.*, 2004a). In such a context, what matters is the relative values of traits of the invader and its competitors rather than with external non-invasive species not involved in competition in the invaded area (Daehler, 2003; Vila & Weiner, 2004).

METHODS

Source material and rearing conditions for laboratory studies

We measured life-history traits under laboratory conditions. We used laboratory strains of *C. catoirii*, C. *capitata*, *C. rosa*, and *B. zonata*, initiated from fruit samples collected in La Réunion, and subsequently reared on artificial diets optimized for each studied species [composition in Duyck & Quilici (2002) and Duyck *et al.* (2004b)], for 30, 3, 51, and 6 generations, respectively. The populations were initiated with 50–100 individuals (*C. catoirii*) or 500–1000 individuals (other species) and later all maintained at several thousands of individuals per generation. Laboratory rearings were conducted at constant temperature (25 ± 1 °C) and photoperiod (L12:D12) supplemented by natural light to maintain twilight conditions (necessary for mating). The temperature of 25 °C was previously shown to be the most favourable for the four studied species (Duyck & Quilici, 2002; Duyck *et al.*, 2004b).

Adult life-history patterns

Thirty newly emerged male–female pairs (< 2 h) of each of all four species were each confined (1 pair per cage) in separate transparent plastic cages (1 L) aerated via meshed openings, in environmental chambers (25 ± 1 °C, 80 ± 10% RH, 4000 lux, L12:D12) (Strader, Pellouailles les Vignes, France). Flies had free access to a diet of sugar and enzymatic yeast hydrolysate (ICN Biomedical, Aurora, IL, USA), and a wet sponge was placed in a container as a water source. An orange table tennis ball (diameter 4 cm), cut in half, and pierced with 24 evenly spaced holes (418 ± 90 μm), containing a piece of mango fruit (*Mangifera indica* L.) and inserted in a plastic base of suitable diameter, was used as a substrate for egg laying. Each morning, new egg cups were placed in all 120 cages to record daily fecundity. On the following day, the number of eggs was counted and each egg cup was replaced to maintain the females in constant conditions, dead males were replaced by new ones from the same cohort. The procedure was repeated until the last female died.

Calculation and analysis of demographic parameters

Daily adult survival and fecundity were combined with previously published data on developmental times and survival rates of immature stages (egg, larvae, and pupae) in the same fly strains at 25 °C [Duyck & Quilici (2002) for *Ceratitis* spp. and Duyck *et al.* (2004b) for *B. zonata*] to compute demographic parameters following standard methods (Carey, 1982; Ebert, 1999). Immature age-specific survivorship rates were interpolated as in Carey (1982). Confidence intervals for demographic parameters were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 1000 times (Efron & Tibshirani, 1993; Caswell, 2001).

Daily fecundity curves were fitted by a log linear model with a Poisson error using GLIM software (Crawley, 1993). Fecundity was fitted as a seventh-order polynomial of age (log number of eggs = $b_0 + b_1x + b_2x^2 ... + b_7x^7$), within each species separately. We chose polynomial functions because they are flexible and provide smooth fitted curves while they impose no constraint on the form of the curve. We dropped the higher-order terms (> 7) because including further terms did not yield a significant increase in goodness of fit in any species. In some species, the term x^7 was non-significant but we nevertheless included it in order to treat all species the same way. We tested for significant differences among species in timing and magnitude of fecundity using the change in deviance between two models: one in which all coefficients are free to vary among species, and one with a common set of coefficients for all species (*F*-test in analysis of deviance, Crawley, 1993). This allowed us to establish that species had significantly different overall fecundity patterns, i.e. polynomial fits do uncover significant differences among species. However, differences in polynomial coefficients have no simple interpretation, so the polynomial equations were used to extract several more informative quantities of interest. All polynomial curves showed a major peak followed by a progressive decrease in fecundity. We characterized these curves using the age at the major fecundity peak, its height, and the age interval during which fecundity exceeded half the peak value. Patterns of senescence in survival were analysed by fitting the Weibull mortality model (hazard function $h(t) = \lambda\alpha t^{\alpha-1}$) (Carey, 2001) using the software GLIM (Crawley, 1993). This formulation includes, as a special case ($\alpha = 1$), the basic exponential model. The senescence parameter (α) exceeds unity when mortality increases with age. Its significance was assessed by a likelihood-ratio test that compared the Weibull model with the exponential model (i.e. with the constraint $\alpha = 1$). To help interpretation, we also provide the mean life expectancy ($\mu = \lambda^{(1-\alpha)}$) and the time interval after which estimated mortality rates are doubled ($d = 2^{1/(1-\alpha)}$).

Egg size and pupal mass

Lengths of 50 randomly chosen eggs, collected from the stock colony ($N > 1000$), were measured for each species within 2 h of oviposition with the graduated graticule of a binocular microscope (× 32). Pupal masses were determined by individually weighing 160 young pupae (< 4 h old) from one cohort of larvae of each species with a precision balance (10^{-4} g). Differences in pupal mass and egg length among species were analysed by analysis of variance, after square-root transformation to ensure normality, and *post hoc* comparisons of means were performed using the Tukey HSD test (5% level of significance).

RESULTS

Data regarding immature development and survival have been obtained from earlier studies on the same strains [Duyck & Quilici (2002) for the three *Ceratitis* species and Duyck *et al.* (2004b) for *B. zonata*]. Pre-imaginal developmental times were significantly different among all species (ANOVA $F_{3,44} = 1799.5$, $P < 0.0001$, Table 1). However, the probability to survive to adulthood was much lower in *C. catoirii* than in the three invading species (ANOVA $F_{3,44} = 528.4$, $P < 0.0001$, Table 1). The four species had significantly different age–fecundity curves ($F_{24,4670} = 64.3$, $P < 0.0001$ by model simplification; all pairs of species are significantly different at $P < 0.0001$, Fig. 1). Knowing that our polynomials capture significant differences among species, and that all of them had a major fecundity peak early in reproductive life, we could use polynomial equations to extract the height, time, and duration of the fecundity peak. The three *Ceratitis* species began to oviposit 5–10 days after emergence, while *B. zonata* began oviposition 20 days after emergence but of the four, oviposited over a longer duration (Fig. 1 and Table 1). *Ceratitis capitata* and *C. rosa* showed similar egg-laying patterns, but the fecundity peak was higher and of shorter duration for *C. capitata* (Table 1). Temporal variation in fecundity of *C. catoirii* was similar to the two other *Ceratitis* spp. but with a very low maximum. Female survival curves decreased in a similar fashion for the four species until *c.* 40 days after emergence, after which, survivorship appeared to be higher in *B. zonata* (Fig. 1). The last females died after 82, 80, 95, and 126 days, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*. Weibull survival parameters were very similar for the three *Ceratitis* species. These three species senesce faster than

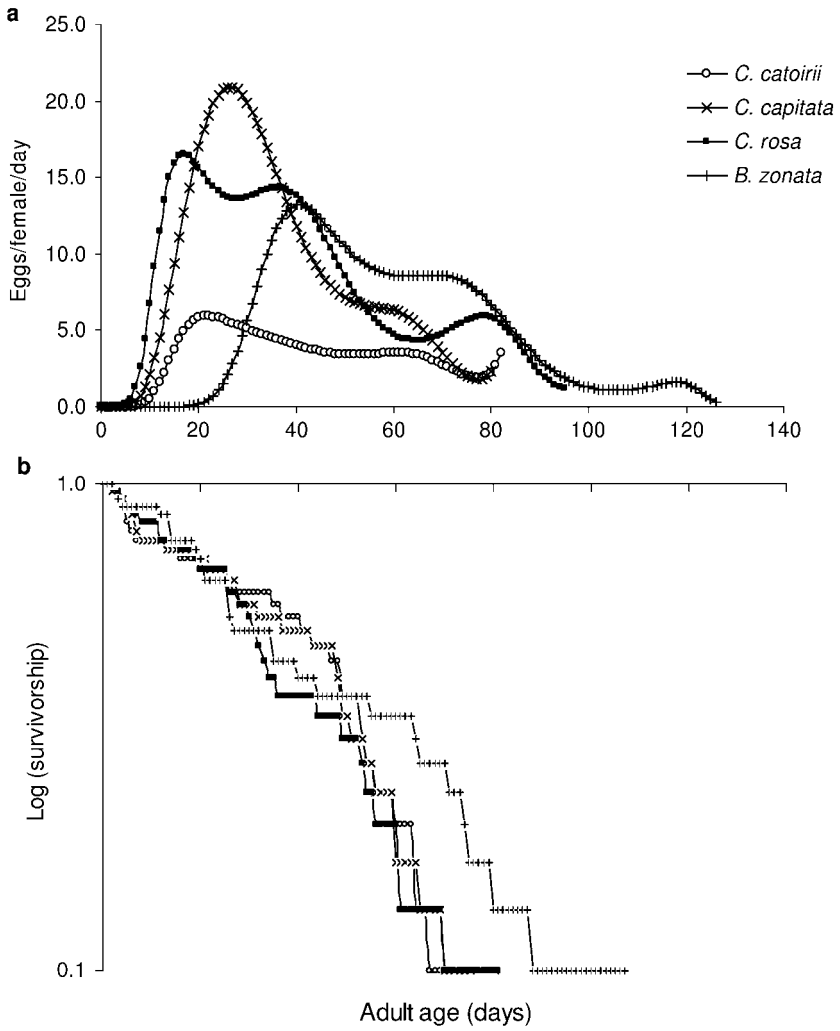

Figure 1 Fecundity and survival patterns in the four species. (a) Number of eggs laid per female per day. Fitted polynomial curves are given. In order to avoid extrapolation, each curve is stopped at the maximum age reached by experimental individuals. (b) Female survivorship of *Ceratitis catoirii*, *C. capitata*, *C. rosa* and *Bactrocera zonata*.

Table 1 Life tables of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa*, and *Bactrocera zonata*. The *P*-value for the Weibull model is the significance of the senescence parameter (H0: $\alpha = 1$) tested by likelihood ratio. The doubling time of mortality is the age at which the death rate is twice its initial value. Cross at max/2 is defined as the two dates when the fecundity curve crosses the value of half maximum fecundity. Data regarding immature development and survival have been obtained from earlier studies on the same strains [Duyck & Quilici (2002) for the three *Ceratitis* species and Duyck *et al.* (2004b) for *B. zonata*] *Means in the same line with the same superscript letter are not significantly different at the 5% level (Tukey HSD).

Parameters	*C. catoirii*	*C. capitata*	*C. rosa*	*B. zonata*
Date of invasion	Resident	1939	1955	1991
Probability to survive from egg to adult*	0.30^{c}	0.73^{ab}	0.75^{a}	0.70^{b}
Mean age at emergence (*d*)*	21.7^{b}	18.4^{c}	23.6^{a}	17.1^{d}
Fecundity parameters:				
Maximum fecundity (eggs/*d*)	5.9	20.9	16.6	13.2
Date of the maximum fecundity (*d*)	21.7	26.5	16.8	40.5
Cross at max/2 (*d*)	[13.9, 50.5]	[15.7, 41.9]	[10.6, 50.5]	[30.9, 80.2]
Parameters of the Weibull model:				
λ	0.006	0.004	0.005	0.008
α	1.366	1.485	1.422	1.265
μ	41.5	42.6	40.0	47.6
Doubling time of mortality (*d*)	6.6	4.2	5.2	13.7
Test: *P*-value	0.02	0.06	0.03	0.12

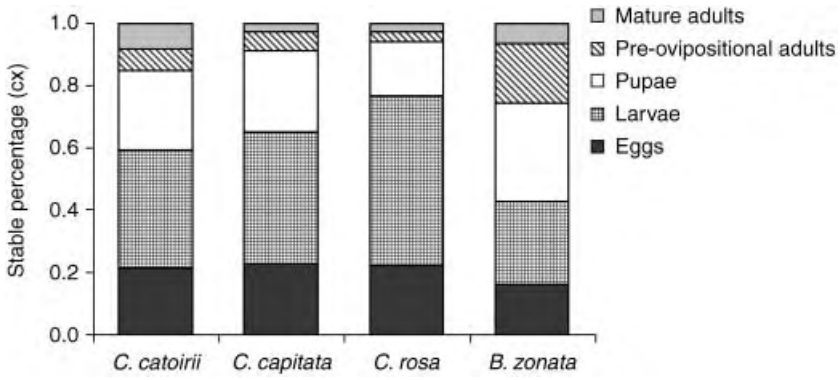

Figure 2 Expected stable age distribution of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa* and *Bactrocera zonata*.

Table 2 Population parameters of *Ceratitis catoirii*, *Ceratitis capitata*, *Ceratitis rosa*, and *Bactrocera zonata*. 95% confidence intervals were obtained by bootstrap (see Methods). *Means in the same line with the same superscript letter are not significantly different at the 5% level (Tukey HSD).

Parameters	Units	*C. catoirii* value [95% CI]	*C. capitata* value [95% CI]	*C. rosa* value [95% CI]	*B. zonata* value [95% CI]
Gross reproductive rate (GRR)	Eggs/female	137.1 [85.2, 174.7]	344.5 [283.3, 405.7]	389.3 [222.6, 536.1]	303.0 [228.3, 367.9]
Net reproductive rate (R_0)	Eggs/female	18.2 [10.6, 25.8]	130.6 [87.5, 162.5]	128.4 [76.1, 177.7]	66.3 [33.7, 101.2]
Intrinsic rate of increase (r)		0.059 [0.048, 0.066]	0.115 [0.104, 0.123]	0.110 [0.097, 0.119]	0.069 [0.057, 0.077]
Intrinsic birth rate (b)		0.128 [0.117, 0.137]	0.121 [0.113, 0.128]	0.120 [0.109, 0.128]	0.096 [0.084, 0.104]
Intrinsic death rate (d)		–0.069 [–0.071, –0.067]	–0.006 [–0.009, –0.004]	–0.010 [–0.012, –0.009]	–0.027 [–0.030, –0.025]
Mean generation time (T)	Days	48.8 [46.3, 51.5]	42.3 [39.9, 44.9]	44.2 [41.8, 47.3]	60.6 [57.7, 64.8]
Average age in stable population ($\bar{a}$)	Days	9.8 [9.0, 10.9]	7.1 [6.6, 7.6]	7.6 [7.1, 8.4]	11.4 [10.5, 12.6]
Mean egg size ± SD*	mm	1.026 ± 0.032^{a}	0.783 ± 0.025^{c}	0.866 ± 0.038^{b}	1.036 ± 0.041^{a}
Pupal weight ± SD*	10^{-4} g	112 ± 14^{b}	94 ± 9^{d}	107 ± 12^{c}	118 ± 13^{a}

B. zonata, for which the senescence parameter is non-significant (Table 1). Similarly, the estimated doubling time of mortality was more than twice as long in *B. zonata* as in the other species.

Ceratitis capitata had the highest net reproductive rate followed by *C. rosa*, *B. zonata*, and *C. catoirii*, respectively (Table 2). Note that demographic parameters previously measured on *C. capitata* (Carey, 1982; Vargas *et al.*, 2000) were similar to our estimates. In our data, the intrinsic rate of increase was similar for *C. capitata* and *C. rosa*, both of which were significantly higher than that of *C. catoirii* and *B. zonata*. The latter species has a significantly longer mean generation time than the other species: 60.6 days compared to 48.8, 42.3, and 44.2 for *C. catoirii*, *C. capitata*, and *C. rosa*, respectively. Immature stages represent the largest part of the theoretical stable age distributions in all species (Fig. 2). However, while the expected proportion of adults was 8% and 6%, respectively, for *C. capitata* and *C. rosa*, it reached 15% in *C. catoirii* and 25% in *B. zonata* (mostly immature adults in the latter). Egg size (ANOVA $F_{3,196} = 665.3$, $P < 0.0001$) and pupal mass (ANOVA $F_{3,636} = 40.3$, $P < 0.0001$) were significantly different among the four species (Table 2). Egg size of *B. zonata* was similar to that of *C. catoirii* and significantly bigger than that of *C. rosa*, itself significantly bigger than that of *C. capitata* (Table 2; Fig. 3). Pupal mass followed the same pattern (except that pupae of *C. catoirii* were significantly lighter than those of *B. zonata*).

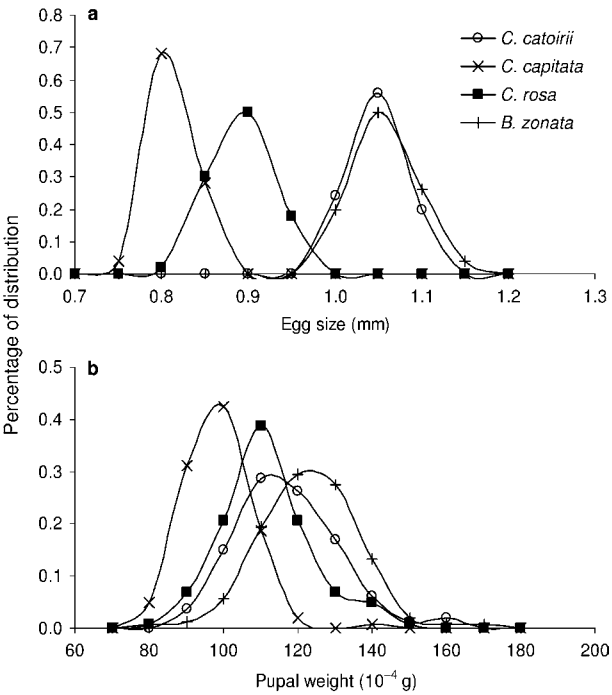

Figure 3 (a) Distributions of egg size (classes of 0.05 mm) and (b) pupal weight (classes of 1 mg) of *Ceratitis catoirii*, *C. capitata*, *C. rosa* and *Bactrocera zonata*.

DISCUSSION

Life histories of tephritid species and trade-offs

The life-history profiles of the three species *B. zonata*, *C. capitata*, and *C. rosa* seem consistent with the idea of a trade-off between traits favouring biomass accumulation and persistence and traits favouring the rapid production of many offspring. The major contrast lies between *B. zonata* and the *Ceratitis* spp., as the former has higher survival and longer duration of the reproductive period, while the other two have higher fecundity and earlier (but shorter) reproduction. Other trade-offs are apparent between the number of offspring on one hand, and both the investment per offspring (as measured by egg size) and the growth (reflected by pupal mass) on the other. These trade-offs are consistent not only with the comparison between *Bactrocera* and *Ceratitis*, but also, to a lesser extent, between *C. capitata* and *C. rosa*. Indeed, *C. capitata* has higher maximum fecundity and shorter pre-imaginal development, but smaller eggs and smaller pupae than *C. rosa*. The latter invests more in each offspring (larger egg size) and pre-imaginal growth, reaching larger pupal masses at the expense of a longer pre-imaginal development. As expected, the intrinsic rates of increase (r) under optimal laboratory conditions are in the order *B. zonata* < *C. rosa* < *C. capitata*, the most pronounced contrast (and the only significant one, i.e. non-overlapping confidence intervals in Table 2) being between the first two. In consistency with the competition–colonization and/or *r–K* trade-off theory (Pianka, 1970; Tilman, 1994), this pattern is the opposite of the competitive hierarchy for these three species (*B. zonata* > *C. rosa* > *C. capitata*, in which, again, the largest contrast occurred between *B. zonata* and the other two; Duyck *et al.*, 2006a).

In contrast, the combination of traits of *C. catoirii*, compared to the other three species, does not support the hypothesis of an interspecific trade-off. Basically *C. catoirii* does not counterbalance its low fecundity by a high survivorship. Although the decreased fecundity and large eggs of *C. catoirii* (as in *B. zonata*) are consistent with a trade-off between quantity and quality of offspring, this large investment per offspring does not seem to provide any advantage, as its mortality during the pre-adult stages is extremely high compared to the other three species. As a consequence, its intrinsic rate of increase under laboratory conditions (r) is approximately half that of the other *Ceratitis* species. Competition experiments have shown that this species is also the poorest competitor of all four species studied (Duyck *et al.*, 2006a). In short, this species is neither a good competitor nor a good colonist.

The differential age of the colonies of the different species may have affected the recorded life-history traits. However, genetic drift and inbreeding have been minimized in all colonies as they were maintained from the beginning using many individuals. Differential adaptation to laboratory conditions could also affect life-history traits. However, this hypothesis predicts that fitness traits would be higher in species cultured in the laboratory for more generations, which is not observed. For example, *C. catoirii* has distinctly lower values for many fitness traits although it is the oldest colony in our laboratory. Finally, another study on *C. capitata* (Muniz, 1987) showed no significant differences in demographic parameters between an old laboratory colony (reared for 19 years) and a field population, suggesting limited effects of adaptation to laboratory conditions.

The imperfect trade-off observed in this study, even between phylogenetically closely related species, is not surprising since perfect trade-offs are the exception rather than the rule in the literature (Stearns, 1992; Reznick *et al.*, 2002; Kneitel & Chase, 2004). Two main causes are traditionally cited for imperfect trade-offs between two traits (Van Noordwijk & Dejong, 1986; Stearns, 1992): first, species may differ by the total amount of resources they are able to extract from the environment rather than by relative allocation to different traits; second, energy may be diverted towards a third trait rather than shared among the two considered. Why the Mascarenes endemic *C. catoirii* does not follow the trade-off common to the three recent invaders remains hypothetical. Anthropogenic influences are relatively recent in La Réunion (four centuries), and populations of *C. catoirii* used to depend on resources from the natural forest habitat in pre-human times. It could invest in some form of specialization to this natural habitat that confers no benefit under 'optimal' laboratory conditions and secondary habitats. This is a mere hypothesis that remains to be tested. More generally, an important caveat for laboratory experiments is that life-history traits and competitive ranks may change depending on conditions, and that actual laboratory conditions may not be optimal for all species. In our case, however, laboratory diets have been optimized for each species, and larval development rates in these diets are better than in the best natural fruits tested to date (P. F. Duyck, unpublished data). Laboratory temperature (25 °C) is also optimal for all four species although *C. rosa* is clearly more cold-tolerant (see Duyck & Quilici, 2002; Duyck *et al.*, 2004b). We are therefore confident that our laboratory conditions are at least very favourable — if not truly optimal — for all species studied.

However, whatever the causes, *C. catoirii* is inferior to the other three species in terms of both colonizing and competitive ability. *Ceratitis catoirii* used to be abundant in cultivated habitats in La Réunion before the arrival of the other species (Orian & Moutia, 1960). Following invasions of *C. capitata*, *C. rosa*, and *B. zonata*, *C. catoirii* has declined and is now very rare in La Réunion, and it has completely disappeared from Mauritius, where the same invasive tephritids have been introduced (Duyck *et al.*, 2006a). All this strongly suggests a case of competitive exclusion.

Competitive ability, traits, and invasion ranks

Based on comparisons between life-history data (this study) and competition data (Duyck *et al.*, 2006a), we can try to identify traits associated with competitive ability. Among the three exotic invasive species, size seems to be a major determinant of competition. Egg size influences larval competition: bigger eggs can reduce larval developmental times and thus confer a resource consumption advantage. This classical pre-emptive effect (Krijger *et al.*, 2001) was observed in our previous work (Duyck *et al.*, 2006a) in the form of relationships between pupal mass and developmental time, both at the interspecific and at the intraspecific

levels: late-emerging pupae were smaller because faster-developing ones had already depleted the resource. Among the three invasive species, a larger adult size also seems to confer an advantage in females competing for ovipositional sites in the same fruit, as pupal size ranks correspond to dominance ranks in interspecific contests among such females (Duyck *et al.*, 2006a). However, size is certainly not the only determinant of competition when considering the endemic species *C. catoirii*. This species lays large eggs, but is dominated by all others in larval competition, owing to a much higher larval mortality. Similarly, its large adult size is not associated to aggressive behaviour in interference contests, during which this species is systematically displaced by all others (Duyck *et al.*, 2006a).

The common hypothesis that successful invaders are often *r*-strategists (Lodge, 1993; Rejmanek & Richardson, 1996) depends on the assumption that competition is not a limiting factor for invasion. This is probably true in many — if not a majority — of cases, when invasions occur in disturbed habitats (Rejmanek, 1996; Lozon & MacIsaac, 1997; Lonsdale, 1999) or habitats devoid of species phylogenetically and/or ecologically similar to the invader. However, with the worldwide increase in the frequency of invasions, the probability that related taxa be introduced successively in the same place increases (Mack *et al.*, 2000; Mooney & Cleland, 2001). In this case, invasion may ultimately depend on the ability to outcompete, or at least to resist competition exerted by, resident species. In line with this hypothesis, in our system, as a result of trade-offs, the intrinsic rate of increase (r) decreases in successive invaders, while competition ability increases. In contradiction with this trend, the endemic *C. catoirii*, a species with very low r, was excluded by the three other species. This is not inconsistent with the hypothesis that invasions were competition-limited, as this species has the lowest competitive ability. However, it illustrates the fact that our hypothesis will only apply as far as trade-offs are respected, as the decrease in r is entirely dependent on its negative correlation with competitive ability.

Could our hypothesis apply to other cases of invasion in the presence of related or similar resident species? In Hawaii, the introduced *Bactrocera dorsalis* (Hendel) largely displaced *C. capitata*, a previously established invader (Debach, 1966). Vargas *et al.* (2000) found that despite a relatively high fecundity, *B. dorsalis* shows a lower intrinsic rate of increase, a bigger size, a delayed onset of oviposition, and a longer life span compared to *C. capitata*. These authors conclude that *B. dorsalis* is less *r*-strategist than *C. capitata*, in agreement with our results. In general, the whole genus *Bactrocera* has a more *K*-orientated profile than *Ceratitis*, which would explain why the former has often displaced the latter during recent invasions, but not the reverse (Duyck *et al.*, 2004a). Such situations are not restricted to tephritid flies however: studying inter-tidal snails, Byers (2000) suggested that competitive ability could be an important characteristic of biological invaders, as did Evans (2004) studying ladybirds, and Vila & Weiner (2004) reached the same conclusion based on a review of competition experiments between resident and invasive plants. Facon *et al.* (2006) also predicted successive waves of invasions by ever-better competitors into the same niche.

Fruit flies in La Réunion are an example of a system in which life-history traits can confer competitive advantages for invading species, though we are not attempting to express a general paradigm applicable to any other system. Yet we believe that these observations should serve as a motivating example of how details of natural history can influence species invasiveness. Obviously, studying four species cannot provide evidence for a general negative relationship between r and invasiveness. However, the limits of our data themselves suggest interesting ways of treating data sets so as to tackle the heterogeneity of invasion cases, frequently cited as the main cause of the scarcity of conclusive results in studies of relationships between traits and invasiveness (Holdgate, 1986; Lodge, 1993; Lonsdale, 1999; Kolar & Lodge, 2001; Facon *et al.*, 2004; Richardson & Pysek, 2006). First, invasions in the absence of likely strong competitors, for example, a predator in an island devoid of predators (Fritts & Rodda, 1998), or *Spartina* in bare mudflats (Davis, 2005), should be distinguished from invasions in the presence of competitors. A possible surrogate, in the absence of competition data, could be the absence or presence of related resident species with similar ecology. Rejmanek (1996) mentioned the fact that 'alien species belonging to exotic genera are more likely to be invasive than alien species from genera represented in the native flora'. This suggests that related residents pose a competitive limit to invasion, and that different mechanisms may underlie invasions in which exotics have to overcome this limit, and those in which they do no have to do so. An important caveat, however, is that the degree of phylogenetic conservation of niche traits seem rather variable among taxa (see the review of Webb *et al.*, 2002) and that other conserved aspects (for example, parasite or enemy assemblages) may be more important than resource overlap and competition in shaping interactions between newly co-occurring congeneric species.

Second, in the case of invasion in the presence of resident competitors, both invasiveness and traits should be considered relative to residents rather than in absolute terms (see Daehler, 2003). For example, *C. capitata* was once invasive in the presence of *C. catoirii* alone, but is no longer invasive in La Réunion since the better competitors *B. zonata* and *C. rosa* arrived. Similarly, in our case, the trait values of the invader are less relevant than the differences between invader and previously established species (e.g. larger pupae or larger eggs relative to residents provide higher competitive ability and trigger invasion).

The last suggestion from our work is to distinguish direct predictions (e.g. r-traits are favourable to colonization in non-competitive contexts) from predictions mediated by a trade-off (r-traits should be negatively correlated with invasion in competitive contexts); the latter, not the former, will depend on how well the assumed trade-off applies to the set of taxa studied, which can be measured directly, as in our Tephritid example.

In conclusion, neither r nor K strategies are likely to be important for invasions in general. In some groups, such as conifers (Rejmanek & Richardson, 1996), invaders have more r-orientated traits than non-invaders. It would be interesting to see whether the majority of conifer invasions happened in the absence of related species and/or in relatively non-competitive habitats, as suggested by the fact that many *Pinus* invasive species are

opportunistic and abundant in disturbed habitats rather than in mature forest (Grotkopp *et al*., 2002). In addition, for invasions that happen in the presence of competitors, invaders may be at the same time better competitors (and worse colonists) than resident species, and better colonists than other potential invaders. Among those candidate invasive species that can overcome competition with residents, the first to invade may indeed be the better colonists. If our conclusions are confirmed by further studies, this framework could provide an important tool in Pest Risk Analysis for the prediction of potential invaders as a function of established regional communities, in addition to the use of measures of environmental suitability of regions to target species (e.g. climatic matching).

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IMPORTANCE OF COMPETITION MECHANISMS IN SUCCESSIVE INVASIONS BY POLYPHAGOUS TEPHRITIDS IN LA RÉUNION

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Abstract. Understanding the strength and modes of interspecific interactions between introduced and resident species (native or previously introduced) is necessary to predict invasion success. We evaluated different mechanisms of interspecific competition among four species of polyphagous fruit flies (Diptera: Tephritidae) from the island of La Réunion: one endemic species, *Ceratitis catoirii*, and three exotic species, *C. capitata*, *C. rosa*, and *Bactrocera zonata*, that have successively invaded the island. Larval competition experiments, i.e., co-infestations of the same fruit, and behavioral interference experiments measuring the ability of one female to displace another from a fruit, were performed among all pairs of the four species. We observed asymmetric and hierarchical interactions among species in both larval and adult interference competition. In agreement with the hypothesis that invasion is competition-limited, the competitive hierarchy coincided with the temporal sequence of establishment on the island, i.e., each newly established species tended to be competitively dominant over previously established ones.

Key words: Bactrocera zonata; *biological invasions;* Ceratitis capitata; Ceratitis catoirii; Ceratitis rosa; *competitive asymmetry; exploitative competition; fruit flies; interference competition; Tephritidae.*

Introduction

Biological invasions pose major problems for biodiversity conservation (Vitousek et al. 1996), one of which is the extirpation of indigenous species by competitive displacement (Elton 1958, Juliano and Lounibos 2005). While attempts to predict invasions based on ecological rules have had some success (Hobbs and Huenneke 1992, Kolar and Lodge 2001, Levine et al. 2004), the importance of interspecific competition in determining when and where invasions occur remains ambiguous. Clearly, competition often takes place between invaders and the recipient community (Dyer and Rice 1999, Shea and Chesson 2002, Levine et al. 2004). However this does not mean that it acts as an important sieve to retain successful invaders from a pool of candidate species. Although this hypothesis or similar ones have been repeatedly put forward (Crawley 1993, Thébaud et al. 1996, Byers 2000, Vila and Weiner 2004), in other cases the emphasis is put on *r*-selected traits and the ability of species to rapidly colonize empty space (Lodge 1993, Rejmanek and Richardson 1996). These two visions seem contradictory, unless one rejects the classical idea of a trade-off between competitive ability and colonization ability (Mac Arthur 1962, Tilman 1994), or, equivalently, envisages invasive species as the "happy few" that happen to override this trade-off. Of course, this apparent contradiction can stem from mixing together different situations: invasions into vacant niches, such as by a predator in a predator-free island (Fritts and Rodda 1998), are by definition not competition limited and should depend only on colonization ability, while invasions into occupied niches can be competition limited. However, for the latter, only empirical studies can tell whether competition is a major determinant of invasion success. Controlled experiments can be useful for this purpose. These experiments give access to competitive responses (the ability of a species to withstand competition exerted by other species) and competitive effects (the negative effects of a species on other species) (Goldberg and Barton 1992). To the extent that laboratory or experimental field results represent phenomena that also operate *in natura*, the competitive effect is expected to determine how an invader may affect established species if it succeeds, while the competitive response, if the competition limitation hypothesis is true, is expected to determine the probability that invasion succeeds. Sets of closely related species successively invading the same territory are ideal situations to test this hypothesis, because competition is expected to be more intense among similar species, especially when they are first brought into contact and have no coevolutionary history (Reitz and Trumble 2002). In addition, within homogeneous

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guilds of animals or plants, competition usually tends to be asymmetrical and organized in a hierarchical way (i.e., transitive [Keddy 2001]). This provides a simple way to test the competition limitation hypothesis: successive invaders should be at higher and higher levels of the hierarchy in competitive response, if such a hierarchy exists.

We here test this prediction in a case study on four species of fruit flies (*Tephritidae*). We are aware that this is only a case study and that many more studies of the same kind would be needed to generalize. Unfortunately, competitive hierarchies have not yet received in invasion biology the attention they have received in plant community ecology (Keddy 2001, Daehler 2003). The choice of Tephritidae as a model system is motivated by several important features. First, the four species studied are all highly polyphagous and show considerable diet overlap (Quilici and Jeuffrault 2001), providing large opportunities of competition. Indeed, species displacements following invasions have been repeatedly observed among Tephritids (Debach 1966, Duyck et al. 2004*a*). Second, a hierarchical mode of competition is suggested by the fact that invasion links (i.e., the ability of species A to invade in the presence of B) seem transitive but never reciprocal in a number of Tephritid invasions worldwide (Duyck et al. 2004*a*). Finally, the history of invasions is well known in our study site: the island of La Réunion (Indian Ocean). One of the species (*Ceratitis catoirii*) is indigenous while the other three (*Ceratitis capitata*, *C. rosa*, and *Bactrocera zonata*) are invaders, whose chronology of introduction is precisely known. Each invader has rapidly grown in numbers once introduced, while previously established species, be they native or previous invaders, declined in at least a part of their range.

The main resource for which interspecific competition can plausibly occur among species of Tephritid flies is the host fruit (Prokopy and Roitberg 1984). In Tephritids, females search for fruit at the appropriate maturation stage and puncture the fruit skin to deposit eggs (Prokopy and Roitberg 1984, White et al. 2000). Eggs hatch and larvae develop within the fruit, then jump out of the fruit onto the ground, where they bury themselves to pupate. Competition can occur in the form of scramble competition among larvae when two species co-infest the same fruit or in the form of direct aggressive interference between females ready to lay eggs in the same fruit. In addition, some features of female behavior may influence the effects of interspecific competition in the field. The ability of a female to detect and avoid fruits that are already infected and the ability to localize available fruits faster than other species can determine how a species tolerates the presence of other, previously established species. In this study we try to compare each of these aspects among the four species in the laboratory.

A potential problem is that the laboratory necessarily represents a single environment that is not representative of the diversity of niches exploited by the species in their natural environment. The four Tephritids we studied are generalist species found on many species of fruits (>350 for *C. capitata* [Liquido et al. 1991]) and in a variety of climatic conditions throughout the island (Duyck and Quilici 2002, Duyck et al. 2004*b*). It is very likely that competition varies among these different niches (Duyck et al. 2004*a*). The study of this variation is a large subject in itself; however, if interspecific competition is to somehow limit invasions, one expects relevant patterns to be found in resources that are both numerically abundant and shared by all species. For this reason we chose to focus our study on a single fruit (guava, a very common fruit in La Réunion, on which all four species have regularly been observed) and a single temperature (25°C, the most favorable temperature for all four species [Duyck and Quilici 2002, Duyck et al. 2004*b*], typical of the cultivated lowlands in La Reunion, where the largest fruit fly populations are found and where new invaders are more likely to be introduced by overseas transport).

Materials and Methods

Fly species and strains

On La Réunion (a volcanic tropical island of the Indian Ocean), four species of polyphagous Tephritidae are currently found. The Mascarene fruit fly *Ceratitis catoirii* is endemic to Mauritius and La Réunion islands (Orian and Moutia 1960, Etienne 1972, White et al. 2000). The Mediterranean fruit fly *C. capitata* was introduced in 1939 and became widespread in La Réunion, while *C. catoirii* became rarer (White et al. 2000). The Natal fruit fly *C. rosa* was first detected in 1955 (Orian and Moutia 1960, Etienne 1972). A similar pattern of successive invasions has been observed in Mauritius, except that *C. catoirii* is now considered extinct on this island, having not been recorded for the last 20 years (White et al. 2000). In La Réunion, the peach fruit fly *B. zonata* was first detected in 1991 but its populations grew massively and spread in 2000 (Hurtrel et al. 2000). This last species is still in the process of expansion. Among the numerous host plants of these species present in La Réunion, four are of particular importance because of their abundance, namely guava (*Psidium guajava* L.), Indian almond (*Terminalia catappa* L.), mango (*Mangifera indica* L.), and strawberry guava (*Psidium cattleianum* Sabine) (Quilici and Jeuffrault 2001). While the four tephritids studied do not have identical host ranges, they share these four main host fruits, as well as many less important ones (Quilici and Jeuffrault 2001). Also, the four tephritids do not have similar climatic niches (Duyck and Quilici 2002, Duyck et al. 2004*b*), but all of them are abundant in the lowlands of the island.

Experiments were conducted with recent laboratory cultures of the four fruit fly species. Techniques for maintenance of these laboratory cultures were described in previous studies (Duyck and Quilici 2002, Duyck et

al. 2004*b*). For experiments on adults, naïve females (with no prior ovipositional experience) were studied at their peak of fecundity (between age 20 and 25 d for the three *Ceratitis* spp. and 40–45 d for *B. zonata*). Rearing conditions were 25°C (±1°), 80% relative humidity (±10%), and 12:12 light : dark photoperiod for all experiments.

Larval competition

The opportunity of interspecific competition depends on the frequency of co-infestations and on the density of larvae within fruits. In order to estimate these parameters, we used a database of 3778 infested fruits of various species, including 786 fruits of guava (*Psidium guajava* L.) and 1196 fruits of Indian almond (*Terminalia catappa* L.), collected in different parts of La Réunion island from 2002 to 2005. Fruits were brought back to the laboratory, individually weighed, and placed on a grid in a closed container layered with sand or sawdust, following standard methods for fruit fly rearings (White and Elson-Harris 1992). Pupae fallen into the sand or sawdust were then counted and species were identified when adults emerged from pupae.

Manipulation trials have often been used successfully to detect asymmetrical competition and hierarchy in plant communities (Goldberg and Barton 1992, Keddy 2001). These experiments usually compare the relative yield of different competing species in the absence and in the presence of competitors (Keddy 2001). We used a similar approach with the four species of Tephritidae in order to assess whether their competitive hierarchy correlates with the ability of a species to invade in the presence of another. Larval competition experiments in the laboratory were conducted with all pairwise combinations of the four species. For each replicate, one or two noninfested guava fruits (total mass of 100 g) were washed and nicked at the surface for introduction of newly hatched larvae (<3 h old) inside the pulp. Fruits were carefully infested with a fine brush under a binocular microscope with 50 newly hatched larvae of only one species (for the control) or 50 larvae of each species (for cross infestations). Such a density of infestation has already been used in several studies on the larval development of Tephritidae (Fitt 1986, Krainacker et al. 1987) and is comparable to observed densities in the field (see *Results*). Our design is additive rather than substitutive (Keddy 2001) and therefore allows us to test the effect of the addition of competitors; this is relevant in our case because fly density in wild-caught fruits co-infested by two or more species exceeds that of mono-infested fruits (see *Results*). However, using our design, the effects of intraspecific and interspecific competition cannot be compared. Infested fruits were put in an open plastic box inside a plastic container, with its bottom covered by a layer of sand to allow for pupation of mature larvae that have jumped from the fruit. From six days after infestation, sand was sifted daily in order to collect pupae. Each pupa was weighed and put in a separate plastic box until emergence of the adult and species determination. Three to seven replicates were done for each pair of species tested and for each control (67 boxes in total). For each parameter and each species, four treatments were used (control and competition with each of the three other species).

Net reproductive rates (R_0), i.e., the expected number of offspring per female in a lifetime, was estimated in order to integrate survival and pupal mass in a single parameter, so as to facilitate comparisons between different treatments. Original R_0 were calculated using established life tables for each species (P. F. Duyck, P. David, and S. Quilici, *unpublished manuscript*). Survival from larva to adult (measured in the experiment) was multiplied by a function of body size that represents the expected number of offspring in an adult lifetime. We used regression equations of fecundity on body size established separately for the four species ($R'_0 = R_0e^{0.0211(p - 112)}$, $R^2 = 0.061$, $P < 0.001$; $R'_0 = R_0e^{0.0506(p - 94)}$, $R^2 = 0.58$, $P < 0.001$; $R'_0 = R_0(0.0082p + 0.1191)$, $R^2 = 0.31$, $P < 0.001$; and $R'_0 = R_0e^{0.0347(p - 118)}$, $R^2 = 0.29$, $P < 0.01$, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*; p = pupal mass, R_0 = original net reproductive rate [$R_0 = 18.2$, 130.6, 128.4, and 66.3, respectively]; R'_0 = estimated net reproductive rate).

In order to test for resource preemption, the relationship between pupal mass and developmental time was analyzed by analyses of covariance (ANCOVA) for each species. Pupal mass was fitted as a function of developmental time (covariate), competition treatment (presence and species of competitor), and their interaction.

Competition results are usually given in terms of relative yield (RY) for plant experiments (Wilson and Keddy 1986, Keddy 2001). As we compared interspecific competition in insects, this indicator was replaced by relative performance (RP), but we kept the same methodology as for plant experiments. Relative performance was calculated for R_0, pupal mass, and survivorship by dividing the value of the target species reared with a competing species by the value of the target species reared alone. Relative performance distinguishes between two components of competitive interactions: the mean response and the mean effect (Goldberg and Barton 1992). For a given target species, the mean response is the mean of RP when reared with competing species, while the mean effect is the inverse of the mean RP of all competing species when reared with the target species. For each parameter (R_0, pupal mass, survivorship), the asymmetry of competition was calculated between species pairs by dividing the RP of the target species by that of the competitor. This definition indicates the direction of asymmetry and differs slightly from the one of Keddy (2001), in which asymmetry is calculated by always dividing the highest RP by the lowest RP of the two competitors.

Behavioral observations

A first assay was carried out to assess the outcome of interference competition for laying sites, i.e., direct interactions between the females of the different species on the same fruit. One half of a strawberry guava (*Psidium cattleianum* Sabine) fruit, cut lengthwise and placed with the skin side exposed, was presented to two females of different species (cage size, $7 \times 12 \times 15$ cm). The number of takeovers, i.e., aggressions by species A leading to the departure of species B from the fruit, was recorded during 30 min. We performed 30–33 replicate assays for each pair of species. Data were analyzed using a Poisson log-linear model (analysis of deviance with Poisson error). Overdispersion was accounted for by using F tests instead of chi-squares to evaluate the significance of changes in deviance (Crawley 1993). The asymmetry of female interference was calculated between each pair of species by dividing the number of takeovers of the target species by that of the competitor.

Other behavioral traits may allow a species to avoid fruit already infested by other species or to localize noninfested fruits faster than other species. Two types of signals may reveal that a fruit is infected: signals from puncture holes made by laying females and host-marking pheromones. In order to determine whether females prefer to lay their eggs in already punctured fruits, we presented two halves of strawberry guava to individual females. One half was intact while the other was artificially punctured 30 times (0.50 ± 0.04 mm) with a needle through the skin to mimic oviposition holes. During 30 min, we recorded the number of landings on each half-fruit and the number of egg-layings in the fruit as well as the occurrence of an "ovipositor dragging" behavior following an egg-laying, previously described as typical of flies depositing host-marking pheromones (HMPs; Prokopy et al. 1978, Papaj et al. 1989). This procedure was repeated with 30 different females for each species.

A second (independent) assay was carried out to test whether females were influenced by prior infestation by females of the same species or of any of the other species. The same procedure as in the previous experiment was employed except that the "treated" half-fruits were not punctured but exposed (in series of 10) to 30 females of the same species or other species during 24 h, while the "control" half-fruits were not. The number of landings and egg-layings were recorded on each half-fruit during 30 min. First, we tested for an intraspecific effect, i.e., whether the behavior of the target species was affected by previous visits by conspecific females. We considered that species with no significant intraspecific response and little ovipositor-dragging behavior did not leave detectable chemical signals or HMPs and used only species with a significant intraspecific effect and a frequent marking behavior (i.e., *C. capitata* and *C. rosa*) to assess interspecific effects. The same experiment as for intraspecific effects was carried out, except that the fruit was first exposed to females of another species (either *C. capitata* or *C. rosa*) and then to the target species. Each test was replicated 30–33 times.

The abilities of females of the four species to localize host fruits were compared using a cylindrical mesh-screened field cage (2.5 m tall $\times$ 3 m diameter). Within the cage, four plants of the non-host *Ficus benjamina* were placed in front of three noninfested washed guava fruits hanging from a metallic support. Twenty females of each species (80 females in total) were released in the cage at the opposite side of the hanging guava fruits. The observer stood behind the *Ficus* plants during 45 min and recorded for each species the number of landings on and egg-layings in the fruits. The procedure was replicated 13 times. The number of landings and egg-layings were analyzed using a Poisson log-linear model. Cumulative time spent on fruits was transformed into percentage of total potential time spent by the 20 females (20×45 min) on fruit prior to angular transformation (arcsine square-root transformed x) and analyzed by one-way ANOVA.

Results

Larval competition

The mean final larval density per fruit in the laboratory experiment measured by the total number of pupae across species was 0.33 ± 0.17 pupae/g (mean $\pm$ SD; range 0.050–0.740). In the field, infested guava fruit produced on average 0.22 ± 0.21 pupae/g (range 0.001–1.661). Irrespective of fruit species, the mean infestation in the field was 0.43 ± 1.07 pupae/g (range 0.001–20.0). The pupal density increased significantly when two (and furthermore three) species were present in a guava fruit ($N = 786$; one species, 73%, 0.16 ± 0.17 pupae/g [mean $\pm$ SD]; two species, 23%, 0.33 ± 0.24 pupae/g; three species, 4%, 0.47 ± 0.33 pupae/g; ANOVA on log-transformed data, $F_{2, 283} = 77.45$, $P < 0.0001$) and in an Indian almond fruit ($N = 1196$; one species, 72%, 0.26 ± 0.28 pupae/g; two species, 26%, 0.44 ± 0.32 pupae/g; three species, 2%, 0.50 ± 0.27 pupae/g; ANOVA on log-transformed data, $F_{2, 1196} = 88.49$, $P < 0.0001$). The final density ratios observed in our experiments and in the field for pairs of species co-infesting the same fruit are given in the Appendix.

Table 1 shows the relative performance of each species reared in all possible pairwise combinations. For most or all species, there is a significant effect of the competition treatment on R_0 (ANOVA, $P < 0.05$ for all species, complete statistics in Table 1), survivorship (ANOVA, $P < 0.05$ except for *C. capitata*), and pupal mass (ANOVA, $P < 0.05$ except for *C. rosa*). Species differed significantly in mean response with respect to R_0 (ANOVA, $F_{3,44} = 8.51$, $P < 0.0005$), survivorship (ANOVA, $F_{3,44} = 6.92$, $P < 0.001$), and pupal mass (ANOVA, $F_{3,40} = 8.45$, $P < 0.005$). However, the mean effect for these three attributes was not significantly different among the species (ANOVAs, $F_{3,44} = 1.22$, $P = 0.31$; $F_{3,44} = 1.55$, $P = 0.21$; $F_{3,40} = 0.88$, $P = 0.46$, respectively for R_0, survivorship, and pupal mass). The

TABLE 1. Relative performance of four species of Tephritidae in all pairwise combinations.

Target species	Control	Competing species (relative performance)				Mean response	ANOVAs for competitive effect		
		Bzon	*Cros*	*Ccat*	*Ccap*		df	*F*	*P*
R_0' (no. eggs/female)									
Bzon	19.41		0.79	0.30	0.71	0.59[a]	3,13	5.1	0.015
Cros	124.27	0.55		0.36	0.50	0.44[ab]	3,15	4.4	0.020
Ccat	10.22	0.02	0.22		0.29	0.15[bc]	3,12	6.8	0.006
Ccap	20.33	0.10	0.04	0.16		0.10[c]	3,11	4.2	0.032
Mean effect		4.00	2.41	3.66	2.00				
Survivorship (rate)									
Bzon	0.70		0.89	0.78	1.03	0.90[a]	3,13	4.0	0.032
Cros	0.82	0.62		0.43	0.64	0.56[ab]	3,15	3.6	0.039
Ccat	0.30	0.05	0.38		0.52	0.32[b]	3,12	4.6	0.023
Ccap	0.39	0.49	0.22	0.60		0.46[b]	3,11	1.7	0.216
Mean effect		2.50	1.79	1.67	1.35				
Pupal mass (10^{-4}g)									
Bzon	91.01		0.95	0.70	0.89	0.85[a]	3,13	5.2	0.014
Cros	102.75	0.84		0.76	0.78	0.80[a]	3,15	2.7	0.085
Ccat	104.89	0.56	0.57		0.72	0.63[b]	3,10	13.0	0.001
Ccap	66.03	0.60	0.56	0.64		0.61[b]	3,9	6.7	0.011
Mean effect		1.43	1.32	1.43	1.25				

Notes: Species whose competitive responses do not significantly differ (Tukey's studentized test, $P < 0.05$) are denoted by common superscript letters. Abbreviations are: R_0', net reproductive rate; *Bzon, Bactrocera zonata*; *Cros*, *Ceratitis rosa*; *Ccat*, *C. catoirii*; *Ccap*, *C. capitata*. The study was conducted on fruit fly species found on La Réunion, a volcanic tropical island of the Indian Ocean.

hierarchy in competitive response was *B. zonata* > *C. rosa* > *C. catoirii* > *C. capitata* except for survivorship, in which the ranks of *C. catoirii* and *C. capitata* were reversed. Note, however, that although the four means are statistically different for all traits, not all pairs of species are, so the hierarchy indicated should be only considered as an overall pattern. The asymmetry of competition and its direction are overall decreasing functions of competitive response ranks (Fig. 1).

For each species, pupal mass decreased with developmental duration and competition treatment (Fig. 2; ANCOVA, $P < 0.05$; see legend for complete statistics), and the interaction was not significant.

Interference competition in the laboratory

Recordings of aggression were strongly asymmetric (Table 2, Fig. 1). The mean number of takeovers (aggressions towards females of other species ending in effective displacement) varied among species (generalized linear model [GLM] with Poisson error, $F_{3,386} = 16.18$, $P < 0.0001$) following the order: *B. zonata* = *C. rosa* > *C. capitata* > *C. catoirii*. Compared with other species, *B. zonata* was overall the species least often driven from fruits by another species (GLM with Poisson error, $F_{3,386} = 3.05$, $P = 0.029$).

Fruit choice experiments

For *C. capitata*, the percentage of visits to artificially punctured fruits was significantly higher (62.4% of all visits, $N = 30$, pairwise *t* tests, $P < 0.05$) than on intact fruits, while for the three other species this percentage did not differ between the two half-fruits (52.5, 50.6, and 47.7% of all visits respectively for *C. catoirii*, *C. rosa*, and *B. zonata*; $N = 30$ for each species, pairwise *t* tests, $P > 0.05$). For all species, the mean percentage of egg-layings was not significantly different between the wounded fruit and the control (45.8, 57.5, 44.0, and 37.8% of all egg-layings, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*; $N = 30$ for each species, pairwise *t* tests, $P > 0.05$).

During our experiments, a behavior of "ovipositor dragging" (as described by Prokopy et al. [1978]) was observed, and its frequency varied among species: it was much higher in *C. capitata* and *C. rosa* than in the two other species (18.2, 72.3, 75.5, and 12.9%, respectively, for *C. catoirii*, *C. capitata*, *C. rosa*, and *B. zonata*). The behavior also differed qualitatively between genera: for the three *Ceratitis* spp. the whole ovipositor was dragged on the fruit surface while for *B. zonata*, only the tip of the extended ovipositor was dragged on the fruit. During this behavior, the four species completed circles on the fruit and repeatedly touched the fruit with their mouthparts. At this stage, *B. zonata* females also stroke the fruit surface with their ovipositors.

Females of *C. rosa* laid significantly less in fruits previously exposed to conspecifics than in control fruits, while the reverse was observed for *C. capitata*, and no significant effect was recorded for *C. catoirii* and *B. zonata* (Table 3a). *Bactrocera zonata* laid less in fruits previously exposed to *C. capitata* or *C. rosa* (Table 3b). The percentage of visits of *B. zonata* was lower on fruits exposed to *C. capitata* than on control fruits, while no difference was observed with fruits exposed to *C. rosa*. No significant effect of interspecific recognition of previous egg-laying was observed between *C. capitata* and *C. rosa*.

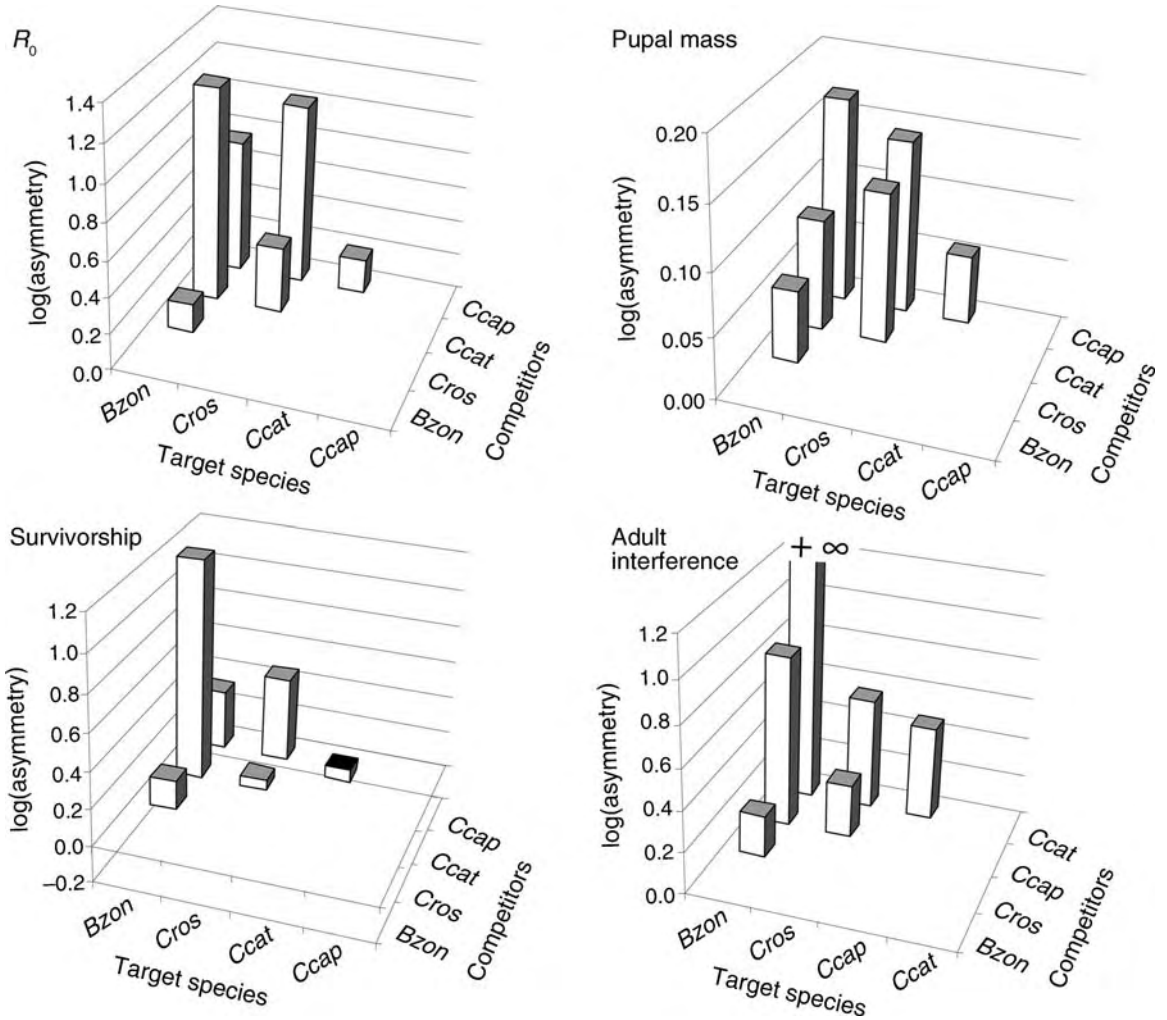

FIG. 1. Competitive asymmetry revealed by pairwise cross-infestation (net reproductive rate [R_0], larval survivorship, and pupal mass) and in adult female interference among the four species of Tephritidae. (See *Methods* for definitions.) Fruit fly species names are abbreviated as in Table 1. For adult interference, the log(asymmetry) *Bzon*/*Ccat* tend to infinity because no displacement of *Bactrocera zonata* by *Ceratitis catoirii* has been observed in any trial. The study was conducted on species found on La Réunion, a volcanic tropical island of the Indian Ocean.

Host location by females

The mean number of landings on fruit (GLM with Poisson error, $F_{3,48} = 12.17$, $P < 0.0001$), layings in a fruit (GLM with Poisson error, $F_{3,48} = 11.28$, $P < 0.0001$), and the mean cumulative time spent on the fruit (ANOVA, $F_{3,48} = 7.37$, $P < 0.001$) varied significantly among species (Fig. 3). *Ceratitis capitata* and *B. zonata* landed significantly more on the fruits than did the two other species. However, the number of egg-layings followed another order: *B. zonata* and *C. rosa* laid more than *C. capitata* and *C. catoirii*. The cumulative time spent on the fruit was longer for *B. zonata* than for the other species.

DISCUSSION

Interspecific competition reduces larval survival, pupal mass, and the potential rate of population increase. Overall, within each species, larval development time and pupal mass are negatively correlated, with late pupae being smaller, with or without allospecific competitors. If all larvae of a given species grew at the same rate, we would expect the opposite pattern, i.e., longer developmental times associated with larger pupae. The observed pattern suggests a competitive preemption of resources within species, i.e., the first larvae to develop benefit from more resource than later ones (Blanckenhorn 1999, Krijger et al. 2001). Adding interspecific competitors does not change the slope of the mass–developmental time relationship but shifts it downward to a variable degree depending on the species involved. Thus, the presence of interspecific competitors has the same effect as having less available resources to begin with. As our experimental densities are comparable to those found *in natura* (especially when two species

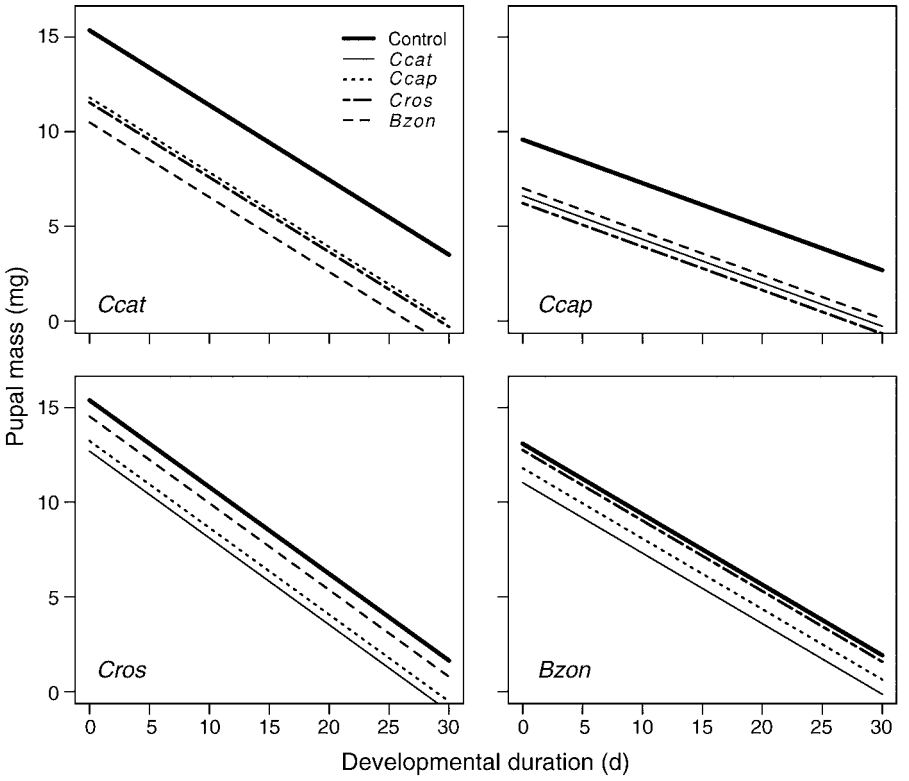

FIG. 2. Relationship between pupal mass and developmental duration for four species of Tephritidae reared alone (control) or in pairwise competition trials (names of competing species are abbreviated as in Table 1). Only regression lines are presented, estimated in the model without interaction. *Ccat*: ANCOVA, developmental duration, $F_{1,5} = 7.0$, $P = 0.04$; treatment, $F_{3,5} = 12.0$, $P = 0.01$; interaction, $F_{3,5} = 1.3$, $P = 0.36$. *Ccap*: ANCOVA, developmental duration, $F_{1,6} = 6.7$, $P = 0.04$; treatment, $F_{3,6} = 28.6$, $P < 0.001$; interaction, $F_{3,6} = 3.4$, $P = 0.09$. *Cros*: ANCOVA, developmental duration, $F_{1,11} = 15.6$, $P < 0.01$; treatment, $F_{3,11} = 6.4$, $P < 0.01$; interaction, $F_{3,11} = 2.8$, $P = 0.09$. *Bzon*: ANCOVA, developmental duration, $F_{1,9} = 17.8$, $P < 0.01$; treatment, $F_{3,9} = 13.5$, $P < 0.01$; interaction, $F_{3,9} = 2.9$, $P = 0.10$.

co-infest the same fruit) in guava or other host fruits, the same kind of competition could occur in the field. The density ratios observed in the field essentially cover all the possible range (0, 1), while we used only a single density ratio (1:1) to measure interspecific competition.

TABLE 2. Mean number of cases where species A was driven out of the fruit by species B during 30 min (n = 30–36 replicates).

Species B (aggressive)	Species A (driven out)				
	Bzon	*Cros*	*Ccap*	*Ccat*	Mean
Bzon		1.61	1.27	0.42	1.10^{a}
Cros	1.00		0.92	1.07	0.99^{a}
Ccap	0.18	0.50		0.67	0.45^{b}
Ccat	0.00	0.30	0.23		0.18^{c}
Mean	0.39^{A}	0.80^{B}	0.81^{B}	0.72^{B}	

Notes: For each pairwise combination means are significantly different (generalized linear model [GLM] with Poisson error, $P < 0.05$) between the two species except for the pairs *Bzon*/*Cros* and *Cros*/*Ccap* ($P > 0.05$). Means followed by different letters are significantly different (GLM with Poisson error, $P < 0.05$). Species names are abbreviated as in Table 1.

TABLE 3. Response of four species of Tephritidae to fruits previously exposed to egg-laying by females of (a) the same species or (b) other Tephritidae species.

Tested species	Sp. to which fruit was previously exposed	Visiting (%)	Laying (%)
a) Egg-laying by same species			
Ccap	*Ccap*	55.2	63.9*
Cros	*Cros*	49.4	29.6*
Ccat	*Ccat*	54.3	49.2
Bzon	*Bzon*	47.6	44.8
b) Egg-laying by other species			
Ccap	*Cros*	48.8	56.5
Cros	*Ccap*	54.6	38.8
Ccat	*Ccap*	44.8	56.3
	Cros	48.2	47.1
Bzon	*Ccap*	31.5**	26.8*
	Cros	44.6	32.9*

Notes: For a given species, percentages followed by one or more asterisks differ significantly from 50% (n = 30–33; pairwise t tests: $^{*}P < 0.05$ and $^{**}P < 0.01$). Species names are abbreviated as in Table 1.

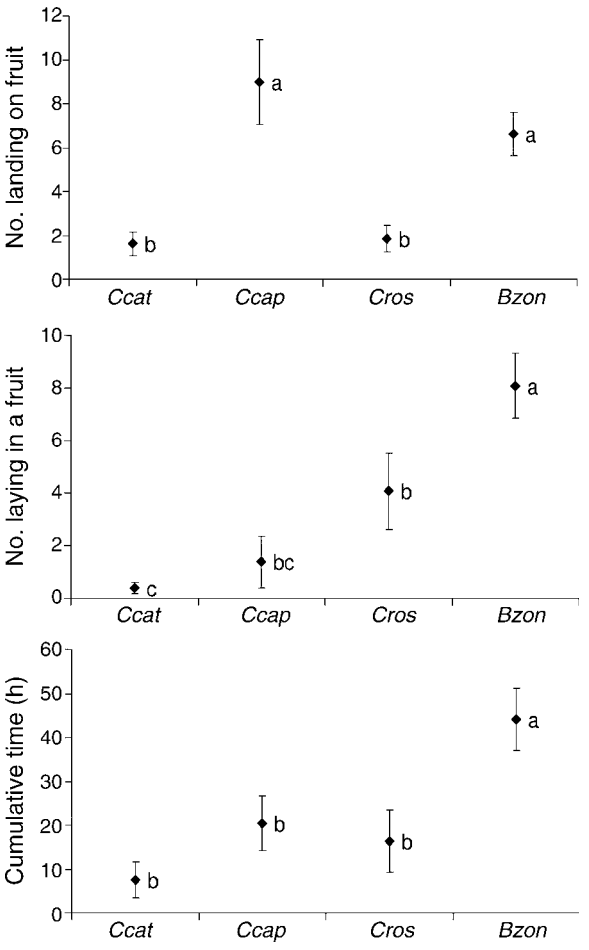

FIG. 3. Comparison of number of landings on fruit, egg-laying on fruit, and cumulative time spent on the fruit per trial by 20 females of each of four species of Tephritidae during a 45-min field cage trial (means ± SE; $n = 13$ replicates). Different lowercase letters indicate significant differences ($P < 0.05$) using a generalized linear model with Poisson error for landings and layings and ANOVA followed by Tukey's studentized test for cumulative time ($P < 0.05$). Species names are abbreviated as in Table 1.

However the final species frequencies we obtained experimentally do not seem unrealistic: for the pair *B. zonata–C. rosa*, the field distribution is roughly symmetric, while experimental ratios lie between 40% and 60%; while for the two pairs involving *C. capitata*, both field and experimental distributions are skewed towards low frequencies of *C. capitata*.

The four species differ in susceptibility to larval competition. Competitive asymmetry is a dominant feature of our data set. As shown in Fig. 1, species can be ordered in a hierarchy whereby competitive asymmetry is always in favor of higher-ranking species. Species have been ordered according to this hierarchy in Fig. 1, *B. zonata* > *C. rosa* > *C. catoirii* > *C. capitata*, so that log-transformed pairwise asymmetries above the diagonal appear positive. The hierarchy is the same for the different components of performance. Only one species pair for one trait (*C. catoirii*/*C. capitata* for survivorship) was inconsistent, as the log asymmetry was slightly negative in this combination (Fig. 1). Competitive responses differ significantly among the four species and overall follow the hierarchy above, although not all pairs of species are significantly different. On the other hand, competitive effect did not vary significantly among species in our experiments, and species ranks were not the same as for competitive responses, although *B. zonata* always came first.

Krijger et al. (2001) showed that short developmental times are associated with superior competitive ability among *Drosophila* species. This trait might confer to *B. zonata* its superior competitive response, as it has a shorter larval development time (mean ± SE: 10.7 ± 1.2 d in the controls) compared to all *Ceratitis* spp. (12.3 ± 1.0 d, 13 ±.0 1 d, and 11.2 ± 0.9 d, respectively, for *C. catoirii*, *C. capitata*, and *C. rosa*) and may therefore preempt resources within the fruit. This also suggests that a different hierarchy may arise at other temperatures as species react differently to temperature. For example at 15°C, the larval developmental time of *B. zonata* becomes longer compared to the three *Ceratitis* spp. (Duyck and Quilici 2002, Duyck et al. 2004*b*).

Aggressive interactions between females at laying sites are highly asymmetrical: of two species, one almost always displaces the other much more than the reverse. As for larval competition, there is a hierarchical arrangement of pairwise interactions between adult females: *B. zonata* > *C. rosa* > *C. capitata* > *C. catoirii* (Fig. 1). A higher-ranking species always displaces a lower-ranking species at higher frequencies than it is displaced. This hierarchy is similar, though not exactly the same, as that observed in larval competition experiments (*C. capitata* and *C. catoirii* have switched positions).

Even with a strict competitive hierarchy for larval competition and adult interference, behavioral strategies could modulate the effects of competition, for example, by allowing weak competitors to lower the probability of being in competition with other species. As suggested by the performance–developmental time relationships discussed above and by the fact that old Tephritid larvae have more severe impacts on young larvae than vice versa (Averill and Prokopy 1987, Dukas et al. 2001), the temporal aspects of resource preemption are important and a species benefits from arriving first at the resource. Two strategies can be envisaged in this context: increased effectiveness in localizing resources or avoidance of previously infested fruits. Our data do not suggest that weak competitors have a better ability to localize the host fruit. On the contrary, in our experimental enclosure (Fig. 3), *Bactrocera zonata*, the best competitor, tended to occupy fruits (and lay on them) for more time than other species. Interestingly, *C. capitata* made more contacts with fruits than other *Ceratitis* species; however it didn't spend more time on it (and didn't lay more often) than *C. rosa*, probably because it was often displaced by *B. zonata*

and *C. rosa* females (Fig. 1). Overall, among the species studied, good competitors (*B. zonata* and *C. rosa*) end up more effective at laying on the resource than poor competitors (*C. capitata* and *C. catoirii*). Our data do not suggest either that poor competitors could limit the adverse effects of competition by avoiding fruits previously infested by other species. None of the species seems to be influenced by the presence of puncture holes on the fruit. However, two of them (*C. capitata* and *C. rosa*) seem to leave detectable chemical signals that influence the laying behavior of conspecifics. These two species display a high frequency of the "dragging ovipositor" behavior, classically associated with host-marking tephritids (Prokopy et al. 1978). Inhibition of oviposition by previous exposure of fruits to conspecifics, here observed in *C. rosa*, has been shown in several tephritids (Prokopy et al. 1978, Diaz-Fleischer and Aluja 2003, Nufio and Papaj 2004) and proved to be caused by host-marking pheromones (Roitberg and Prokopy 1987, Nufio and Papaj 2001). Surprisingly, *C. capitata* seems slightly attracted rather than inhibited by exposed fruits in our study. However, this species is known to show context-dependent attraction or avoidance behavior (Papaj et al. 1992, Prokopy and Roitberg 2001). Although we have no direct evidence that HMPs are involved in the attraction (*C. capitata*) or avoidance (*C. rosa*) of exposed fruits, HMPs are likely candidates. On the other hand, neither *B. zonata* nor *C. catoirii* seem to discriminate fruits previously exposed to conspecifics. The low frequency of "ovipositor-dragging" behavior has already been observed in other species of the subfamily *Dacini* that do not produce HMPs and interpreted as a remnant of ancestral marking behavior (Prokopy and Koyama 1982, Fitt 1984). Interestingly, *B. zonata* detects and avoids signals left by *C. capitata* and *C. rosa,* while the response of *Ceratitis* species to each other's signals is nonsignificant. Again, this behavior is expected, if anything, to increase the resistance of *B. zonata* to competition exerted by other species rather than the reverse. We acknowledge, however, that these experiments conducted in artificial settings may not necessarily represent field conditions.

Each newly arrived species successfully invaded La Réunion in the presence of the previously established native or exotic species (Orian and Moutia 1960, Etienne 1972, White et al. 2000). This can be summarized as follows: *B. zonata* > *C. rosa* > *C. capitata* > *C. catoirii* where the "more than" sign denotes the ability of a species to establish new populations, grow in numbers, and spread in territories occupied by another species. A previous review on invasions by fruit flies (Duyck et al. 2004*a*) has already shown that such links tend to be directional, not reciprocal, within this family, suggesting some deterministic mechanisms behind invasion sequences. In La Réunion, these ranks also reflect the current relative abundance of the species on several important host fruits in the lowlands where they coexist, *B. zonata* being generally dominant while *C. catoirii* has become very rare (Duyck et al. 2004*a*). We should mention, however, that *C. rosa* is currently the only species with important populations in the highlands.

The results of our competition experiments together support the view that the ability to withstand interspecific competition exerted by resident species has been a major limiting factor for invasions in the Tephritid system studied here. Indeed, invasive species tend to have higher ranks than previously established species in the hierarchy for one or both forms of competition (scramble and interference). *Bactrocera zonata*, the most recently established species, appears dominant in most of the forms of competition studied. Its large body size may be an advantage in exploitative as well as in interference competition. At the other end, the endemic species, *C. catoirii*, also has a large size but gains no advantages from it, either in exploitative or interference competition. Although it can exert strong competitive effects on other species at the larval stage, it does not resist well against allospecific competitors. This might doom this species to extinction in the presence of invasive tephritids, as suggested by its currently extreme rarity in the island of La Réunion and its reported extinction in the nearby island of Mauritius (White et al. 2000). Based on this study, a future invasive polyphagous Tephritidae in La Réunion should have a better performance in larval competition and/or a more efficient, aggressive behavior than the four resident species. Both traits could be enhanced by a larger body size and a shorter larval developmental period, which can be obtained via a higher investment per offspring (larger egg size).

Other studies have already shown that invasive species can have superior competitive ability than native species (Juliano 1998, Byers 2000, Vila and Weiner 2004). Our study confirms and extends these results, showing that these mechanisms are repeatable and consistent in a group of phylogenetically and ecologically close species in the same habitat. As reported in experimental (Case et al. 1994, Holway 1999) and theoretical (Amarasekare 2002) works, our study suggests an important role of interference in the invasion success. Recently, Yasuda et al. (2004) demonstrated that intraguild predation, an extreme form of interference, contributes to the invasion success of ladybirds. Our study also suggests that interference and scramble competition abilities are not necessarily in trade-off, as illustrated by invasive ants (Holway 1999).

Finally, one important limitation of competition experiments is to ignore niche differentiation between species. In essence, we have established a clear competitive hierarchy in guava at 25°C, which would logically allow the prediction of sequential invasion and exclusion in a homogeneous landscape containing only this niche. The natural environment in La Réunion (or in any invaded country) is certainly not like this, and patterns of niche differentiation among species must be studied to get a full view of possible events in terms of invasions and coexistence or exclusion of species. For example, the large

populations of *C. rosa* found in the highlands of La Réunion, where no other species are found, are suggestive of a climate-dependent change in competitive hierarchy. Host fruit, although less well known, might have similar effects. Generalization to other conditions will be needed in future studies. To a certain extent it is even surprising that competitive abilities in an environment only chosen to be nutrient-rich (guava) and thermally optimal (25°C) for all species adequately predict the invasion sequence. Why couldn't a species directly invade the environment where it can be dominant, irrespective of its competitive ability in optimal conditions? We suggest that in the case of Tephritid flies in La Réunion, and possibly many other invasion cases, propagule pressure is concentrated into a particular habitat. In La Réunion this habitat consists of anthropized, cultivated lowlands (a rich and warm niche relatively similar to our experimental conditions). This habitat may act as a filter niche, in which any candidate invader must be able to establish a viable population (and therefore to resist competition by residents) before spreading to other habitats. Further studies are needed to test this hypothesis.

Acknowledgments

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APPENDIX

A figure showing the distributions of final density ratios when two species were present in a fruit (*Ecological Archives* E087-104-A1).